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By
John E. McCosker

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ABSTRACT. A classification of the genera of the apodal family Ophichthidae is proposed on the basis of internal and external morphology, with particular emphasis on osteological characters. Specimens of 89 ophichthid species from 44 genera and comparative material from ten other apodal families were prepared for osteological examination, usually by a trypsin-based staining and clearing technique, and critically compared. Forty-nine ophichthid genera are recognized and are distributed among six tribes in two subfamilies. Diagnostic characters for the recognition of genera include the shape and condition of elements of the gill arch and hyoid arch, number and placement of branchiostegal rays along the hyoid, suspensorium elements, neurocrania, dentition, pectoral girdle elements, cephalic pore patterns, lateral line ossification, fin placement, and morphometric characters. The Ophichthidae are defined on the basis of their numerous overlapping branchiostegals, supraorbital canals united by a transverse commissure through the fused frontals, first and second epibranchial interconnections, absence of a palatine, and the separation of the pterygoid from the vomer. A monophyletic origin of the family from a congrid-like ancestor is proposed. An evolutionary history of the Ophichthidae is suggested, in which the subfamily Myrophinae has separated into two tribes and the subfamily Ophichthinae has radiated into four tribes. The validity of the family name Ophichthidae is discussed. The family names Ophisuridae, Myridae, Myrophidae, Muraenichthyidae, Echelidae, Neenchelidae, Aoteidae, Acanthenchelyidae and Sphagebranchidae are synonyms of the name Ophichthidae. A comparison is made between an ophichthid classification based primarily on osteology and the previous classification, based primarily on external morphology. The results of two computer-programmed classification schemes of species relationships within a single tribe are compared with a classification developed using traditional methodology. Alternate hypotheses are proposed to explain the log-normal inverse relationship between genera and the distribution of species among genera in the Ophichthidae.

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Figure 1. An early illustration of an ophichthid eel, presumably *Ophisurus serpen* from Mattioli's *Commentaires* (1568).

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By

John E. McCosker

UCTION

)phichthidae comprise a large family of 'ossorial eels limited to continental shelf)f all tropical and subtropical oceans. The hidae contains more than 200 species ;tributed among 49 genera, representing the greatest diversity of anatomical spe-)ns within a single apodal family. The ance of many ophichthids to snakes has :hem the common name of "snake-eels," ng with the morays, have evoked many ent legends among tropical coastal peo- rhaps the earliest illustration identifiable)phichthid (fig. 1) was that of Mattioli . 388, probably based on an adult *Ophi- ɜrpens*. The first described ophichthid *Muraena ophis*, was the second apodal innaeus' *Systema Naturae* (1758).

The taxonomic treatment of the Ophichthidae, and of apodal fishes in general, has been in constant flux since the eighteenth century, and only within the past two decades has a coherent concept of the Ophichthidae become realized. Previous theories of the interrelationships of ophichthid genera have been based on such trivial characters as fin position, dentition types and coloration. It is now generally accepted that the osteology more conservatively reflects the phylogeny of a group and is less affected than external morphology by minor evolutionary adaptations. The unsatisfactory state of the classification of the ophichthids has been recognized by numerous authors (Myers and Storey, 1939; Myers and Wade, 1941; Gosline, 1951a; Smith, 1964; Rosenblatt and McCosker, 1970; Robins and Robins, 1971; Castle, 1972) most of whom have concluded that an osteological revision of all included genera was necessary for a proper understanding of the family. The aim and scope of this study have been directed to that objective.

History of Ophichthid Classification

The 218 years since Linnaeus' (1758) description of the first ophichthid species have witnessed a plethora of generic and specific names applied to the Ophichthidae. The first generic name properly applied to an ophichthid was *Ophichthus* (Ahl, 1789), which should more properly have been written *"Ophichthys"*. The emendations of Ahl's generic spelling by subsequent authors have resulted in confusion over the generic and familial names. This problem was briefly treated by Gosline (1951a: p. 298) and is further illuminated in the following discussion.

The treatment of apodal taxonomy was in constant flux during the eighteenth and nineteenth centuries, which accounts for much of the lack of uniformity in nomenclature. Swainson's (1838) treatment of the eel-like fishes was based largely on Cuvier's work (1817), and was the first attempt at an arrangement of the eels into family groups. Swainson (p. 215) designated the *"Muraenidae* (as) having two branchial spiracles in their ordinary position, and the *Sphagebranchidae*, or sea eels, where the branchial spiracles are either close together or united into one." Confusion ensues on the following page where the family name Gymnarchidae is apparently considered synonymous with the Symbranchidae, and further evidenced in his discussion (p. 218) of the gill openings, by his statement that "among the *Gymnarchidae*, or sea eels, for instance, they are close together and united under the throat as in *Sphagebranchus*." Swainson divided the Muraenidae into two subfamilies, the Anguillinae and the Muraeninae, both of which contained species now known to be ophichthids. McClelland (1844) realigned the apodal classifications of Swainson and Cuvier and created the family Ophisuridae to include eels with a rayless caudal containing the genera *Leptognathus (=Ophisurus), Ophisurus,* and *Ophithorax (=Ophichthus)*. Kaup (1856a,b) disregarded most of McClelland's classification without comment, but did retain the name Ophisuridae. Kaup divided the apodal fishes into two "sections". These were the Cryptomycteres (containing only the Ophisuridae) which included those eels with labial nostrils, and the Phaneromycteres which contained all other apodal families. The ophisurids were divided into three subfamilies, the Ophisurinae, the Sphagebranchinae, and the Myrophinae (containing *Myrus, Myrophis,* and *Muraenichthys)*. Bleeker, in his *Systema Muraenorum Revisum* (1865), recognized the family Ophisuroidei and considered the Myrophinae (as Myriformes) to be a su
of the family Congroidei. Günther (187
siderably revised previous classification b
ing the majority of the known eels into
family, the Muraenidae, which he divid
ten "Groups". The Ophisuridae of earlier
was divided into two groups, the Ophic
containing those species with a rayless
[comprising the genera *Liuranus (sic)*
single species and *Ophichthys* with at l
species], and the Myrina containing those
rayed caudal (comprising *Myrus, Myrophi*
myrus, Chilorhinus, and *Muraenichthys*)
ther's groups were elevated to family r
Jordan and Davis (1891). The Myrinae
the family Echelidae (Jordan and Davis con
Myrus a synonym of *Echelus)* and the (
thyina of Günther (actually, the Ophisurc
Bleeker) became the Ophisuridae. Unc
concerning the synonymy of *Myrus* and
resulted in the changing of the name Eche
Myridae by Jordan and Evermann (1896)
Jordan and Snyder (1901). The family
Ophichthyidae, derived from Günther's (
thyina, first appeared in Jordan and Ev
(1896). The authors rejected the name O
dae and considered *Ophisurus* a synon
Ophichthus.

Validity of the Family Name

Confusion relating to the spelling
Ophichthyidae with a "y" relates to the
tion by earlier authors of Ahl's (1789) spe
Ophichthus. The generic name is from th
ὄφις, meaning snake, and ἰχθύς
ing fish, and would more correctly hav
written *Ophichthys*. Bleeker, Günther, an
classicists emended Ahl's generic spelli
Jordan and Gilbert, 1882), but Jordan
later co-authors returned to Ahl's origin
ing. The retention of the original spelling
generic name but the usage of the emend
ily name is illogical, and according to th
national Code of Zoological Nomenclat
correct, as Gosline (1951a) has pointed ou
recent authors, with few exceptions, ha
"Ophichthidae" and *"Ophichthus"*.

A serious difficulty however exists, con
the earlier family names proposed by S
and by McClelland. The inconsistencies in
son's usage of Sphagebranchidae would in
it as a family name. Although *Sphageb*
Bloch (1795) was then a valid genus and
an ophichthid, *Gymnarchus*, a gymnarch

'n not to be an apodal fish. The prob-
:ognizing McClelland's usage of *Ophi-*
as avoided by Gosline who stated that
or not *Ophisurus* is a valid genus is a
nenclatorial question. Consequently I
to use for this family, at the present
little-known and possibly invalid name
ae." The logical solution to this nomen-
lemma seems to be the invoking of the
owers of the International Commission
ical Nomenclature. The suppression of
used name Ophisuridae in favor of the
recognized name Ophichthidae would
in the interests of stability.

al Studies of the Ophichthidae

1912) was the first to attempt an osteo-
finition of the Ophichthidae. Most im-
his emphasis on the fused frontals of
hthids, congrids, and relatives has re-
a fundamental character in our con-
eel evolution. The other osteological
identified by Regan ("caudal vertebrae
verse processes" and "maxillaries articu-
ethmoid near the end of the snout")
ibed certain members of the family. His
of the congrids from the ophichthids,
sis of their long and slender rather than
eural spines, was also an important ob-
Trewavas' (1932) apodal classification
llowed Regan's characterization of the
ls. For nearly two decades, subsequent
l studies dealt only with superficial
. An exception was that of Myers and
39) who noticed the overlapping of the
egal rays in ophichthid species. They
ut that these rays are similar to the
lia" described by Parr (1930) in echelid
hat basis, and other external morpho-
nilarities, Myers and Storey suggested
Echelidae might be merged with the
dae.

(1950, 1951a, 1951b, 1952), in a series
analyzed the species referred to the
and the Ophichthidae. His osteological
Kaupichthys diodontus (1950) demon-
it its osteology precluded its inclusion
ne family with *Muraenichthys cookei*.
(p. 312-314) that *K. diodontus* differs
sutured frontals and non-overlapping
egal rays, as well as several other char-
ich later proved to be non-definitive.
specimen of *Echelus myrus*, Gosline
e to further define the Echelidae, but
that species of *Myrophis* and *Muraen-ichthys* might be referred to the Ophichthidae, to comprise the subfamily Myrophinae, on the basis of their "basket-like arrangement of the numerous, long branchiostegal rays." In a following paper, Gosline (1951b) described the osteology of *Chilorhinus brocki* (=*C. platyrhynchus*) and related it to *Kaupichthys diodontus*. He suggested that the external similarities of species of *Kaupichthys*, *Chilorhinus* and ophichthids are "the result of parallel evolution and not of close genetic relationship." His prediction that *Echelus*, once examined on an osteological basis, would prove to be confamilial with *Kaupichthys* was incorrect (Gosline, 1952; Böhlke, 1956a).

Gosline (1951a), in a more comprehensive paper, prepared the first diagnostic treatment of the Ophichthidae. His study, however, was limited to those species occurring in the Hawaiian area and thus did not include several critical genera. He compared the Ophichthidae with the Congridae (primarily *Conger*), and concluded that the ophichthid conditions are derived from, and more advanced than, those of their more primitive congrid ancestors. Two subfamilies within the Ophichthidae were recognized (the Myrophinae and the Ophichthinae) although osteological differences other than the caudal skeleton were not defined. In a subsequent paper, Gosline (1952) described the morphology of *Echelus myrus* in detail and concluded that it was referable to the ophichthid subfamily which contained *Myrophis* and *Muraenichthys*. On that basis he changed the subfamilial name of the Myrophinae to Echelinae. The results of that study did not alter his earlier (1951a) diagnosis of the family.

Subsequent studies dealing with ophichthid osteology followed Gosline's (1951a) general definition of the family, but amended his diagnosis to include genera that he had not examined. Böhlke (1960) added *Pseudomyrophis*, and provisionally *Neenchelys*, to the Ophichthidae.In doing so, he expanded the familial diagnosis to allow the following: posterior nostrils either lateral or labial; maxillary articulation variable in position along the ethmoid; pharyngeal openings of the branchial clefts may be reduced; transverse processes of the caudal vertebrae either present or absent.

Nelson's (1966a) analysis of apodal gill arch conditions found most ophichthids to be "distinguished in having the proximal ends of the dorsal parts of the first and second arches connected through a continuous cartilage, a peculiarity not present in any other of the eel families studied." Certain generic lineages were identified

on the basis of their gill arch configurations. Nelson's (1966b) study of the osteology of *Neenchelys buitendijki* confirmed Böhlke's earlier supposition of its placement within the Ophichthidae. Nelson separated the ophichthids from the congrids in the following manner: posterior nostril usually opening on the ventral surface of the upper lip; tongue adnate; branchiostegal rays overlapping along the midventral line; supraorbital canals united by the transverse frontal commissure; neural spines absent. Castle's (1972) osteological study of *Benthenchelys cartieri* summarized the diagnoses from Gosline's, Böhlke's, and Nelson's earlier works, but did not contribute to or amend their diagnoses.

Familial Synonymy of the Ophichthidae

The Ophichthidae, as currently recognized, includes several families which were until recently considered distinct. The basis and validity of studies resulting in these actions are discussed below.

The family Neenchelidae was erected by Bamber (1915) to contain *Neenchelys microtretus*, a new genus and species from the Red Sea. It was considered to be closely related to the Muraenesocidae as defined by Regan (1912). A second neenchelid, *N. buitendijki*, was described by Weber and de Beaufort (1916) from the Indo-Australian archipelago. The family received no further definitive treatment until Böhlke (1960), on the basis of Bamber's description, suggested that *Neenchelys* may be related to species of *Pseudomyrophis* and thus properly be considered an ophichthid of the subfamily Echelinae (sensu Gosline, 1951a, 1952). The collection of adequate material of *N. buitendijki* and its osteological examination by Nelson (1966b) supported Böhlke's prediction. Nelson's (1967) examination of the holotype of *N. microtretus* confirmed the recognition of the Neenchelidae as ophichthids in the subfamily Echelinae (herein considered as Myrophinae).

The Acanthenchelyidae also belongs in the Ophichthidae. Family recognition was short-lived, consisting of Jordan, Evermann, and Clark's (1930) elevation of *Acanthenchelys* Norman (erroneously attributed to Regan) to family status, but this was largely ignored by later authors. Randall and Robins (1966) relegated *Acanthenchelys* to the synonymy of *Ophichthus*, an action which is followed here.

The Aoteidae are provisionally included in the Ophichthidae. The Aoteidae were first recognized as ophichthids by Castle (1967), who refe
single aoteid species to the genus *Muraei*

The family Echelidae (=Myridae, Myn
Myrophidae, and Muraenichthyidae), has
catch-all group with a checkered hist
echelids were considered congrid or n
socid relatives by most nineteenth cen
thors. Bleeker (1865), for example, co
the Myriformes (containing *Myrophis*,
and *Muraenichthys*) to be a subfamily
Congroidei. Kaup (1856a, b) was except
placing considerable importance on th
nostril condition, and in allying the Myn
with the Ophisurinae as a single unit wh
cluded the congroids and relatives. Tw
century authors considerably expanded the
phidae (which was to become known
Echelidae, fide Jordan and Evermann, 1
include as many as 22 genera at variou
(Schultz and Woods, 1949). The dissection
large and cumbersome family was initia
Myers and Storey (1939), and was follo
Schultz and Woods (1949) and by Gosline
1951a, b, 1952). Myers and Storey noted th
ence of accessory branchiostegal rays (the
stegalia" of Parr, 1930) in both ophichthi
echelids, but were hesitant to merge the
without an extensive anatomical exami
Gosline (1951a) established the similarities
two families on an osteological basis and in
the genera *Myrophis* and *Muraenichthys*
Ophichthidae to comprise the subfamily
phinae. His subsequent (1952) osteologi
amination of *Echelus myrus* resulted in its
sion into the family, and the replacement
name Myrophinae with Echelinae. The
study has demonstrated that Gosline was
in considering the Myrophines to be ophic
but erred in including *Echelus* with the
phinae. Although certain authors have co
to recognize a family Echelidae for the
with caudal rays (e.g., J. L. B. Smith, 1962;
1968), no convincing arguments have be
posed which would merit familial sep
Blache's (1968: 1501) continued usage
name Echelidae, with the justificatio
"... nous sommes également, tout à fait,
de cette position et nous ne conservons
famille des Echelidae, que pour des raiso
ficielles de commodité taxonomique,"
illogical and incorrect.

Further substantiation of the inclusion
Echelidae with the Ophichthidae is evide
the leptocephalus larval stage. (The l
phalus of *Neenchelys* has not been ide

hali display evolutionarily conserva- that could prove useful in phylogen- ations (Castle, 1965, 1967), yet the generic and specific identification and has precluded their usage in t is important to note, however, that logy of ophichthid leptocephali re- nily grouping fairly well. Castle (1965) th (unpub. MS) have diagnosed the eptocephalus as moderately elongate own, characteristically possessing gut or loops which usually accompany the pronephric ducts, conspicuously /ith patches of chromatophores which occur on the head, at various points it, and often on the myosepta, lateral ine, and dorsal and anal bases, and moderate to blunt tail. Castle (1965: ·d that "the pectoral remains obvious larval life, probably even in those which show loss of the pectoral in and adult." Phylogenetic implications ric level would therefore be further ı this conservative larval condition if gestion proves correct. For example, identification of *Leptocephalus Mur-* ıp. is based on a leptocephalus pos- hort, rounded pectoral fin (Castle, 2F, G), not unlike that of *Myrophis* 6; Castle, 1965: figs. 3e-f).

st to the above mentioned families, phenchelyidae was incorrectly synony- the Ophichthidae. This family, known he holotype and damaged paratype *ıhenchelys brachialis* Fowler, was syn- 'ithout comment with the Ophichthi- .llister (1968: 85). Robins and Robins re-erected the family on the basis of osteological examination of the para- have shown its affinities to be with ae and referred it to the superfamily *Macrocephenchelys* displays several uite divergent from the Ophichthidae, ıe extensive ossification of the bran- ıtus (yet there is no lower pharyngeal , the absence of the transverse frontal of the cephalic lateralis system, and e of eight stout branchiostegal rays ·lete palatopterygoid arch.

Ophichthid Classification

g of nominal taxa below summarizes ıic conclusions of this study. Full de- f new taxa and complete generic syn- presented later in this paper.

Subfamily Myrophinae
- Tribe Benthenchelyini
  - *Benthenchelys* Fowler 1934
- Tribe Myrophini
  - *Ahlia* Jordan and Davis 1891
  - *Muraenichthys* Bleeker 1853
    - Subgenus *Muraenichthys* Bleeker 1853
    - Subgenus *Scolecenchelys* Ogilby 1897
  - *Myrophis* Lütken 1851
  - *Neenchelys* Bamber 1915
  - *Pseudomyrophis* Wade 1946
  - *Schismorhynchus* McCosker 1970
  - *Schultzidia* Gosline 1951

Subfamily Ophichthinae
- Tribe Callechelyini
  - *Aprognathodon* Böhlke 1966
  - *Callechelys* Kaup 1856
  - *Letharchus* Goode and Bean 1882
  - *Leuropharus* Rosenblatt and McCosker 1970
  - *Paraletharchus* McCosker 1974
- Tribe Sphagebranchini
  - *Achirophichthys* Bleeker 1865
  - *Apterichtus* Duméril 1806
  - *Caecula* Vahl 1794
  - *Cirricaecula* Schultz 1953
  - *Hemerorhinus* Weber and de Beaufort 1916, *incertae sedis*
  - *Ichthyapus* de Barneville 1847
  - *Lamnostoma* Kaup 1856
  - *Stictorhinus* Böhlke and McCosker 1975
  - *Yirrkala* Whitley 1940
- Tribe Bascanichthyini
  - *Allips* McCosker 1972
  - *Bascanichthys* Jordan and Davis 1891
  - *Caralophia* Böhlke 1955
  - *Dalophis* Rafinesque 1810
  - *Ethadophis* Rosenblatt and McCosker 1970
  - *Gordiichthys* Jordan and Davis 1891
  - *Leptenchelys* Myers and Wade 1941
  - *Phaenomonas* Myers and Wade 1941
- Tribe Ophichthini
  - *Aplatophis* Böhlke 1956
  - *Brachysomophis* Kaup 1856
  - *Cirrhimuraena* Kaup 1856
    - Subgenus *Cirrhimuraena* Kaup 1856
    - Subgenus *Jenkinsiella* Jordan and Evermann 1905
  - *Echelus* Rafinesque 1810
  - *Echiophis* Kaup 1856
  - *Elapsopis* Kaup 1856
  - *Evips* McCosker 1972
  - *Leiuranus* Bleeker 1853

Malvoliophis Whitley 1934
Myrichthys Girard 1859
Mystriophis Kaup 1856
Ophichthus Ahl 1789
Subgenus *Ophichthus* Ahl 1789
Subgenus *Microdonophis* Kaup 1856
Subgenus *Centrurophis* Kaup 1856
Subgenus *Coecilophis* Kaup 1856
Ophisurus Lacépède 1800
Phyllophichthus Gosline 1951
Pisodonophis Kaup 1856
Pogonophis Myers and Wade 1941
Quassiremus Jordan and Davis 1891
Scytalichthys Jordan and Davis 1891
Xyrias Jordan and Snyder 1901

METHODS

Taxonomic Methods

Osteological examinations, whenever possible, were based on entire stained and cleared specimens. Rare specimens and holotypes were studied by gill arch removal and radiographic examination. Radiographs were prepared using a General Electric 40 KV x-ray unit and Kodak Industrial Type M film. Radiographs were either examined under a dissecting microscope or from photographic enlargements. Stained and cleared gill arches or entire specimens were prepared using the trypsin-preparation method of Taylor (1967) and, in certain instances, the modifications of Miller and Landingham (1969). Neurocrania were prepared by dissection, soaking in a 5-7 percent potassium hydroxide (KOH) solution to remove the flesh, and staining in an alizirin bath. Sutures along the dry skulls became more apparent during examination when painted with pure glycerin using a fine camel's hair paint brush. Certain skulls were disarticulated in a 7-10 percent KOH solution to better identify certain sutures. Drawings were made using a camera lucida attachment on a Wild dissecting microscope.

Gill arch terminology is that of Nelson (1969). Bone terminology follows that of Asano (1962) with certain modifications that are identified in the section dealing with bone complexes.

The following measurements, used in the generic key and descriptions, are defined as follows:

Head length. Measured from the snout tip to the posterodorsal point of the gill opening.

Trunk length. Measured from the posterodorsal point of the gill opening to mid-anus.

Tail length. Measured from mid-anus to the tail tip.

Inclination of the suspensorium. Th sorium is considered to be "anteriorly if the angle formed by the midlines o mandibular and the mandible (when t is closed) is greater than 90°. If the an than 90° the suspensorium is conside "posteriorly inclined". This measuremen what subjective, and made either fr graphs or observations of stained an specimens under the dissecting microsc

All fish lengths are listed as total len eric descriptions and diagnoses were adults unless otherwise stated.

ABBREVIATIONS

Anatomical Abbreviations

A - anus; **an** - anterior nostril; **AR** - ana **B_1** - first basibranchial; **BO** - basioccipi branchiostegal ray; **BS** - basisphenoid; ceratobranchial; **CE** - centrum; **CH** - c **Cl** - cleithrum; **Co** - coracoid; **CTP** - trans cesses of caudal vertebrae; **CX** - cartila tension of terminal vertebra; **D** - denta dorsal fin origin; **DR** - dorsal fin ray; **E** **E_1** - first epibranchial; **EH** - epihyal; **EN** al; **EO** - epiotic; **ET** - ethmoid portion o illoethmovomer; **EX** - exoccipital; **F** - fro gas bladder; **GH** - glossohyal; **GO** - gill **H** - heart; **H_1** - first hypobranchial; **H** arch; **HH** - hypohyal; **HY** - hypural; **H** mandibular; **I** - intestine; **I_2** - second in gobranchial; **IM** - intramuscular bone; orbital pore; **IO** - interopercle; **L/D** - r length to depth; **LL** - lateral line; pharyngeal tooth plate; **MX** - maxilla; **NA** - neural arch; **NS** - neural spine; **OP** **OR** - orbit; **P** - parapophysis; **PA** - parie parasphenoid; **PD** - pneumatic duct; **P** goid; **PL** - pleural rib; **pm** - preoperculo lar pore; **PO** - preopercle; **pop** - pre pore; **por** - postorbital pore; **POR** - p **PR** - pectoral fin rays; **Pt** - pterygioph pterotic; **PTS** - pterosphenoid; **Q** - qua stomach; **SA** - sagitta; **Sc** - scapula; **S** cleithrum; **so** - supraorbital pore; **SO** - pital; **SOC** - supraoccipital crest; **SO** ercle; **sp** - surface sensory papillae; **S** otic; **stp** - supratemporal pore; **tp** - temp **UH** - urohyal; **UP** - upper pharyngeal to **V** - vertebra; **VO** - vomer.

Distributional Abbreviations

EA - eastern Atlantic; **EP** - eastern Pa central and Indo-west Pacific; **M** - Medi **WA** - western Atlantic.

ıl Abbreviations

ing abbreviations are used in reference l examined: ıdemy of Natural Sciences of Philadel- **M** - Bernice P. Bishop Museum; **CAS** - Academy of Sciences; **DANA** - Carls- ts DANA-Ekspeditioner, Marinbiologisk um Charlottenlund Slot, Denmark; **IA** - Museum at Sydney; **LACM** - Los An- nty Museum; **MCZ** - Museum of Com- Zoology, Harvard University; **MNHN** - National d'Histoire Naturelle, Paris; useo Civico di Storia Naturale, Genoa, **JSP** - Museu de Zoologia, Universidade 'aulo, Sao Paulo, Brazil; **RU** - Rhodes , Grahamstown, South Africa; **SIO** - ıstitution of Oceanography; **SU** - Stan- ersity, also listed as **SNHM** for Stanford listory Museum, specimens now de- t the CAS; **TABL** - Southeast Fisheries liami, Florida; **UCLA** - Fish Collection, nt of Zoology, University of California ngeles; **UMML** - Rosenstiel School of ıd Atmospheric Science of the Univer- ami; **USNM** - National Museum of Nat- ɔry, Smithsonian Institution, Washing- ; **ZMA** - Zoölogisch Museum Amster-

xamined

ɔelow is the material utilized for osteo- amination in this study. The specimens ɔed by tribes and listed alphabetically ch tribe. Following each specific name ɹseum abbreviation, museum catalogue ıumber of specimens, range of the total of the specimen(s) involved. Abbrevia- CS, stained and cleared by the Taylor ypsin technique; GA, gill arches re- tained and cleared; H, hyoid removed; preparation; X, radiograph. Specimens ɔnly for vertebral counts are not in- this listing.

ıthidae - Benthenchelyini. *Benthenchelys* ⅁ANA 3735, 2(105-115mm), CS.

ıthidae - Myrophini. *Ahlia egmontis*, SIO 268), S; SIO 71-266, 1(337), CS. *Muraen- :hilensis*, SIO 65-645, paratype, 1(248), 65-655, paratype, 1(276), CS, 1(292), S. *hthys gymnopterus*, SIO 69-276, 1(129), , CS. *Muraenichthys gymnotus*, SIO 69- ı4), CS. *Muraenichthys macropterus*, SIO l(181), CS. *Myrophis plumbeus*, SIO 69-371, 1(182), CS. *Myrophis uropterus*, CAS 13971, 1(159), CS; BPBM 27209, 1(182), CS. *Myrophis vafer*, SIO 68-242, 1(193), CS, 2(265-325), S. *Pseudomyrophis micropinna*, SIO 60-72, 1, head and trunk only, CS. *Pseudomyrophis nimius*, ANSP 110150, 1(350), CS. *Schismorhynchus labialis*, CAS 24687, 5(114-137), CS. *Schultzidia johnstonensis*, SIO 69-267, 1(138), CS.

Ophichthidae - Callechelyini. *Aprognathodon platyventris*, SIO 68-393, paratypes, 2(312-330), CS. *Callechelys bilinearis*, SIO 70-376, 1(260+), CS. *Callechelys cliffi*, SIO 61-247, 1(218), GA, H, X; SIO 65-281, 1(298), GA, H, X. *Callechelys eristigmus*, SIO 65-185, paratype, 1(552), GA, H, X; SIO 65-354, paratype, 1(431), CS. *Callechelys galapagensis*, UCLA 64-40, paratype, 1(767), GA, H, X. *Callechelys holochromus* (holotype of *Cryptopterygium holochroma)*, USNM 154994, 1(801), X. *Callechelys luteus*, SIO 68-497, 1(1038), H, X. *Callechelys marmoratus*, SIO 69-269, 1(286), CS, 1(340), S. *Callechelys melanotaenius*, SIO 69-269, 1(401), CS. *Callechelys muraena*, TABL Oregon 2819, 1(235), GA, H, X. *Callechelys nebulosus*, SIO 71-197, 1(283), CS. *Callechelys springeri* (holotype of *Gordiichthys springeri)*, USNM 121604, 1(372), X. *Callechelys striatus* SIO 71-165, 1(430), H, X. *Letharchus velifer*, holotype, USNM 31458, 1(396), X. *Letharchus rosenblatti*, SIO 67-40, paratype, 1(248), CS. *Leuropharus lasiops*, holotype, SU 57313, 1(174), GA, X. *Paraletharchus opercularis*, UCLA 64-38, 1(435), GA, X. *Paraletharchus pacificus*, SIO 65-321, 2(276-369), CS.

Ophichthidae - Bascanichthyini. *Allips concolor*, holotype, CAS 13967, 1(375), GA, X. *Bascanichthys panamensis*, SIO 71-98, 1(425), CS; SIO 71-224, 1(295), CS, 1(510), S. *Caralophia loxochila*, SIO 70-228, 1(445), CS; SIO 70-376, 1(238), CS. *Dalophis imberbis*, SIO 72-290, 1(440), GA, X. *Ethadophis byrnei*, holotype, SIO 67-31, 1(508), GA, X. *Ethadophis merenda*, holotype, SIO 65-47, 1(530), GA, X. *Leptenchelys vermiformis*, holotype, USNM 101785, 1(115), X. *Phaenomonas cooperae*, CAS 13964, 2(451-549), CS. *Phaenomonas pinnata* SIO 65-348, 1(375), CS, 1(375), S.

Ophichthidae - Sphagebranchini. *Apterichtus caecus*, MSNG 41058, 1(435), X. *Apterichtus flavicaudus*, SIO 69-364, 1(300), CS. *Caecula pterygera*, USNM 206375, 1(232), CS. *Cirricaecula johnsoni*, paratype, USNM 141189, 1(325), CS. *Ichthyapus ophioneus*, SIO 70-376, 1(337), GA, X. *Ichthyapus selachops*, SIO 61-232, 1(400), CS, 1(400), S; SIO 65-343, 1(234), CS. *Ichthyapus vulturis*, holotype, ZMA 104.153, 1(240), X; SIO 69-

366, 1(446), GA, X. *Lamnostoma kampeni*, SU 24593, 1(435), GA, X. *Lamnostoma orientalis*, CAS 13959, 1(205), CS; CAS 13968, 1(229), CS. *Stictorhinus potamius*, MZUSP 8959, paratype, 1(289), CS. *Yirrkala kaupi*, SU 26827, 1(345), GA, X. *Yirrkala lumbricoides*, CAS 13969, 1(346), CS; paratype of *Y. chaselingi*, IA 16190-601, 1(560), X. *Yirrkala misolensis*, CAS 13965, 1(335), CS. *Yirrkala tenuis*, SIO 71-165, 1(370), CS. *Yirrkala* sp., BPBM 11858, 1(306), CS.

Ophichthidae - Ophichthini. *Aplatophis chauliodus*, UMML 27209, 1(165), CS. *Brachysomophis sauropsis*, SIO 69-267, 1(323), CS; SIO 69-271, 1(197), CS. *Cirrhimuraena macgregori*, SIO 68-434, 2(291-317), CS. *Cirrhimuraena taeniopterus*, CAS 13962, 1(445), GA, H, X. *Elapsopis cyclorhinus*, SIO 69-267, 1(268), CS, 1(475), GA. *Echelus myrus*, SIO 69-369, 1(449), dissected. *Echelus pachyrhynchus*, SIO 69-370, 1(355), CS. *Echiophis* sp., UMML 29144, 1(298), CS. *Evips percinctus*, holotype, CAS 13966, 1(125.5), GA, X. *Leiuranus semicinctus*, SIO 61-132, 1(195), CS; SIO 69-268, 1(243), CS; SIO 69-273, 1(344), S. *Malvoliophis pinguis*, IA 3646, 1(470), CS. *Myrichthys colubrinus*, SIO 69-272, 1(345), CS. *Myrichthys maculosus*, SIO 68-497, 1(390), CS; SIO 69-272, 1(310), CS. *Myrichthys xystrurus*, SIO 65-335, 1(420), S; SIO 65-354, 2(243-268), CS. *Myrichthys* sp., SIO 34-371, 1(386), CS. *Ophichthus altipinnis*, CAS 14647, 1(915), GA, X. *Ophichthus cephalazona*, SIO 69-279, 2(230-330), CS. *Ophichthus erabo*, CAS 13960, 1(480), GA, H, X. *Ophichthus ophis*, SU 51724, dissected. *Ophichthus rutidodermatoides*, CAS 28727, 1(330), CS. *Ophichthus triserialis*, SIO 61-193, 1(230), CS; SIO 69-252, 1(800), S, prepared skeleton. *Ophichthus zophochir*, SIO 60-304, 1(217), CS; SIO 65-166, 1(310), S, 1(340), S. *Ophisurus serpens*, RU 76-78, 1(325), CS. *Phyllophichthus xenodontus*, SIO 69-273, 2(270-305), CS. *Pisodonophis boro*, SIO 69-281, 1(410), CS. *Pisodonophis cancrivorus*, SIO 69-307, 1(345), CS. *Pisodonophis cruentifer*, MCZ 34529, 1(235), CS. *Pisodonophis daspilotus*, SIO 72-73, 1(251), CS. *Pogonophis fossatus*, SIO 61-227, 2(232-249), CS. *Quassiremus evionthas*, UCLA 64-19, 1(283), GA, X. *Quassiremus nothochir*, SIO 65-334, 2(271-342), CS. *Scytalichthys miurus*, CAS 13970, 1(235), CS. *Xyrias revulsus*, holotype, SU 6476, 1(890), GA, X.

Comparative Material - Non-ophichthids. The following material was stained and cleared with two exceptions. These, *Gymnothorax mordax* and *Muraenesox coniceps*, were examined from prepared skeletons.

Anguillidae. *Anguilla rostrata*, SIO 1(210).

Muraenidae. *Anarchias galapagensis*, 345, 1(130). *Echidna nebulosa*, SIO 59- *Enchelycore bayeri*, CAS GVF 1957-1 *Gymnothorax castaneus*, SIO 65-291 *Gymnothorax mordax*, SIO skeletal c 1(ca. 1 meter). *Gymnothorax panamensi* 239, 1(180). *Gymnothorax schismato* CAS GVF 1958-13, 1(265). *Muraena le* SIO 65-354, 1(165). *Uropterygius necti* 65-302, 1(175).

Simenchelyidae. *Simenchelys parasiti* 68-479, 1(295).

Derichthyidae. *Derichthys serpentinus*, 239, 1(140).

Serrivomeridae. *Serrivomer sector*, SIC 1(305).

Nemichthyidae. *Nemichthys scolopace* 65-243, 1(440).

Heterenchelyidae. *Pythonichthys asod* type, UMML 23481, 1(290).

Muraenesocidae. *Muraenesox conice* skeletal collection, a large adult.

Moringuidae. *Moringua ferruginea*, SIC 1(305).

Congridae. *Ariosoma gilberti*, SIO 3(175-190). *Conger cinereus*, SIO 68-531 *Gorgasia punctata*, SIO 62-270, 1(365). *conger* sp., SIO 62-42, 1(235).

Xenocongridae. *Chlopsis apterus*, LACI 2(152-155). *Kaupichthys hyoproroides*, SI 2(150-190).

Statistical Methods

Comparisons of vertebral means and were made with a standard "t" test. T puter-programmed grouping techniqu used to compare inter- and intra-gene tionships within the Callechelyini. The modifications of a clustering technic weighted variable group method (W Sokal and Michener (1958), and of a group analysis (REGROUP) devised b (1957). Each will be discussed briefly, the original sources should be referr further information is desired.

Wormuth's (1971) modification of used by him in ommastrephid squid ta was used to identify the interspecific ships of 18 of the 21 species of the Calle Cluster analysis is a technique widely numerical taxonomists, wherein each sp individual) is termed an operational ta

). The program, as described by Wor-
'1), operates in the following manner:

a matrix of *m* characters by *n* OTU's
ıp and the values in each row are
lized using row means and variances.
he standardized matrix *(m x n)* a
moment correlation coefficient is
ed. This matrix expresses the rela-
s between all possible pairs of
quantitatively. At this point a cluster-
ocedure is employed to extract a
representation of the information
ed in the correlation matrix. Any pair
s which has a higher correlation with
her than either has for any other
put together as a group. An average
on coefficient is computed for each
nd it is, thenceforth, treated as a
OTU. In the WVGM a variable num-
ew groups are formed on each cycle.
end of each cycle, correlation coeffi-
e recomputed based on the previous
On any single clustering cycle two
ves are available. One permits only
of two OTU's to form prior to recom-
of the correlation matrix if their
ation lowers the overall group cor-
value by less than a preselected
As the results of both alternatives
number of trials were very similar,
r option was selected for its shorter
ation time. The levels at which
are formed are plotted. The graphi-
esentation of the results is termed a
am.

characteristics used in program WVGM
allechelyini are presented in tables 8

it group analysis was devised by Fager
dentify communities of species on the
heir co-occurrence in samples (Fager
wan, 1963; Fager and Longhurst, 1968)
modified for taxonomic purposes by
d Weed (1963) and by Fager (1969).
pecies pair, the program calculates an
affinity. Fager and McGowan (1963)
this index does not follow the hyper-
distribution exactly, and have there-
ed it with the geometric means of the
of common characteristics, corrected
umber of characteristics recorded for
, such that:

$$I = \frac{J}{\sqrt{A \times B}} - 1/2 \sqrt{B}$$

index of affinity, J = number of com-
cteristics, A and B = total characteris-
led for species A and species B, and where B = A. All characteristics are equally weighted. From the matrix of species pairs which is generated the largest possible group of species is selected. A "breakpoint" is selected such that pairs of species in which I is greater than or equal to that point are considered to show affinity. For example, the selection of 0.500 as a breakpoint would group species which share somewhat more than "half" their characteristics. In this study, breakpoints of 0.500 and 0.600 were utilized, the latter appearing to give more reasonable groups without involving excessive alternative and unnatural groups. Once selected, the largest group is removed and the procedure is continued until all possible groups are formed. Where two or more groups of equal size are possible, the program selects the one for which the sum of species pairs' affinity indices is largest. Intergroup relationship can be calculated using the sum of characteristics shared by members of each group as a fraction of the total possible connections (see fig. 44). Inter-group similarity is therefore directly related to this fraction.

It should be noted that the computer programs used are each affected by the amount of, and manner in which, data are presented. The sensitivity of each program increases with increased data input. REGROUP is particularly insensitive to continuous data (e.g., vertebral and branchiostegal ray numbers, body proportions) and treats each data interval equally. WVGM, by contrast, takes account of continuous data in calculating a correlation coefficient, but is somewhat more insensitive to dichotomous and trichotomous data. The characteristics used in each program are identified in tables 8 and 9.

OSTEOLOGY AND FUNCTIONAL ANATOMY

In the following section the osteology of *Ophichthus zophochir* is described and illustrated in detail. The bone complexes are treated separately, each beginning with a description of the condition of *O. zophochir* and followed by a discussion of variations and specializations among other genera within the family. Also included in this section are discussions of the otoliths and of the gas bladder and digestive tract conditions of certain ophichthids.

Ophichthus zophochir was selected as the species with which other ophichthids are compared because it possesses the majority of ophichthid anatomical characters in a rather generalized state. This is not meant to imply that *O. zophochir* is the most primitive ophichthid, but rather

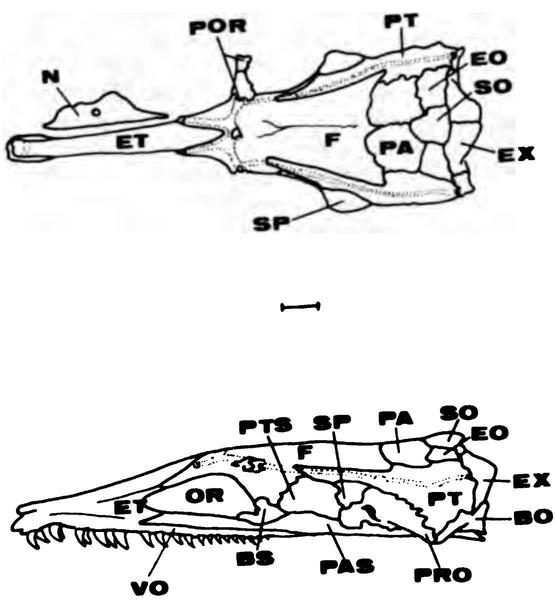
that by being generalized, and not specialized by means of extreme anatomical reduction, it provides a framework for comparison and discussion.

Neurocranium

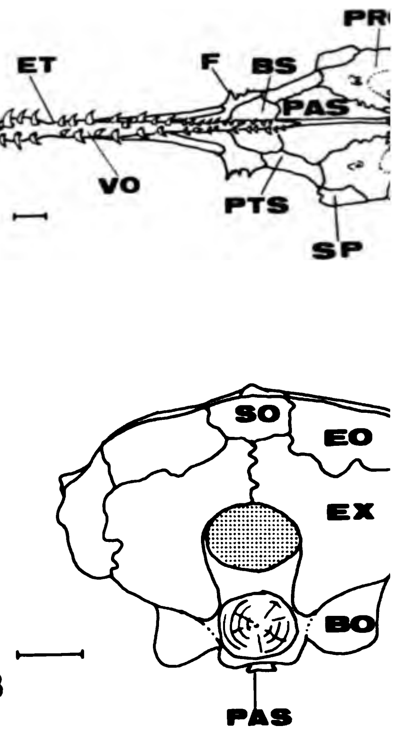
The neurocranium of *O. zophochir* is completely ossified and well fused along the cranial sutures. The skull is stout, rather elongate, and truncate posteriorly. The neurocranium of an adult *O. zophochir,* like that of most anguilliforms, is small in relation to the total length of the fish. It occupies 5.5 percent of the TL, yet the neurocrania of more elongate ophichthids, such as *Phaenomonas cooperae,* occupy as little as 1.3 percent. Various aspects of the neuro-

cranium of *O. zophochir* are illustrate
2 and 3. Described below are the ele
posing the neurocranium.

Premaxilloethmovomer. The prem
moid, and vomer are fused into a
plex (PEV) articulating posterodorsal
frontal and posteroventrally with th
noid, and forming the anterior ma
orbit. The anterior portion of the PE
maxillae, has been shown to be se
the vomer in other eels, including *A*
guilla (Norman, 1926), *Derichthys*
(Beebe, 1935), and *Coloconger sch*
1967), yet in ophichthids there are
sutures separating the elements, and t
limits can only be determined ont
The premaxillary portion is expande



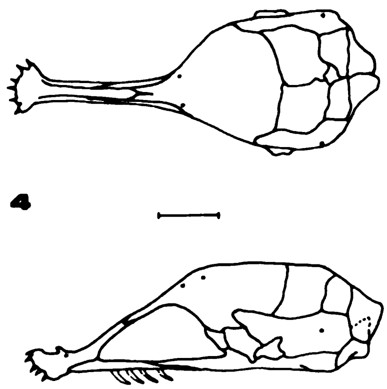
2

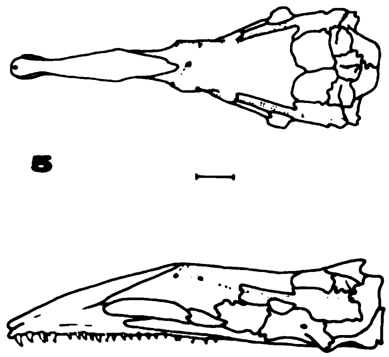


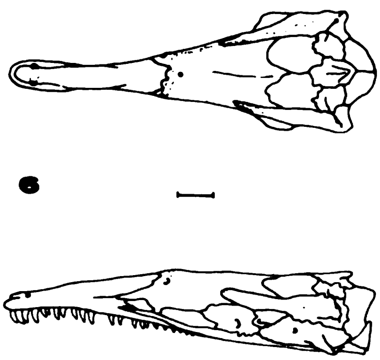
3

Figure 2. Neurocranium of *Ophichthus zophochir,* SIO 65-166. Upper, dorsal
lower, left lateral view. Scale represents 1 mm. Stippled lines represent cephalic lat
canals. Abbreviations are: BO, basioccipital; BS, basisphenoid; E, ethmoid portion of
maxilloethmovomer; EO, epiotic; EX, exoccipital; F, frontal; N, nasal; OR, orbit; PA, par
PAS, parasphenoid; POR, postorbitals; PRO, prootic; PT, pterotic; PTS, pterosphenoid
supraoccipital; SP, sphenotic; VO, vomer.

Figure 3. Neurocranium of *Ophichthus zophochir,* SIO 65-166. Upper, ventral
lower, posterior view. Scale represents 1 mm. Abbreviations are as in Figure 2. Sagitta
is outlined by stippled line.







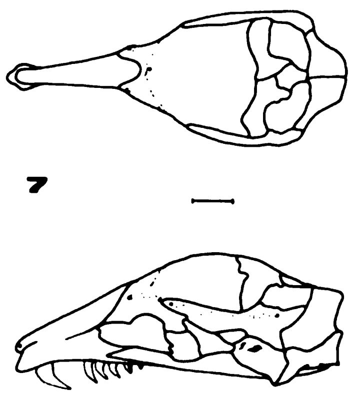


Figure 4. Neurocranium of *Benthenchelys cartieri*, DANA Sta. 3735. Scale represents 1 mm.

Figure 5. Neurocranium of *Myrophis vafer*, SIO 68-242. Scale represents 1 mm.

Figure 6. Neurocranium of *Muraenichthys chilensis*, SIO 65-655. Scale represents 1 mm.

Figure 7. Neurocranium of *Callechelys marmoratus*, SIO 69-629. Scale represents 1 mm.

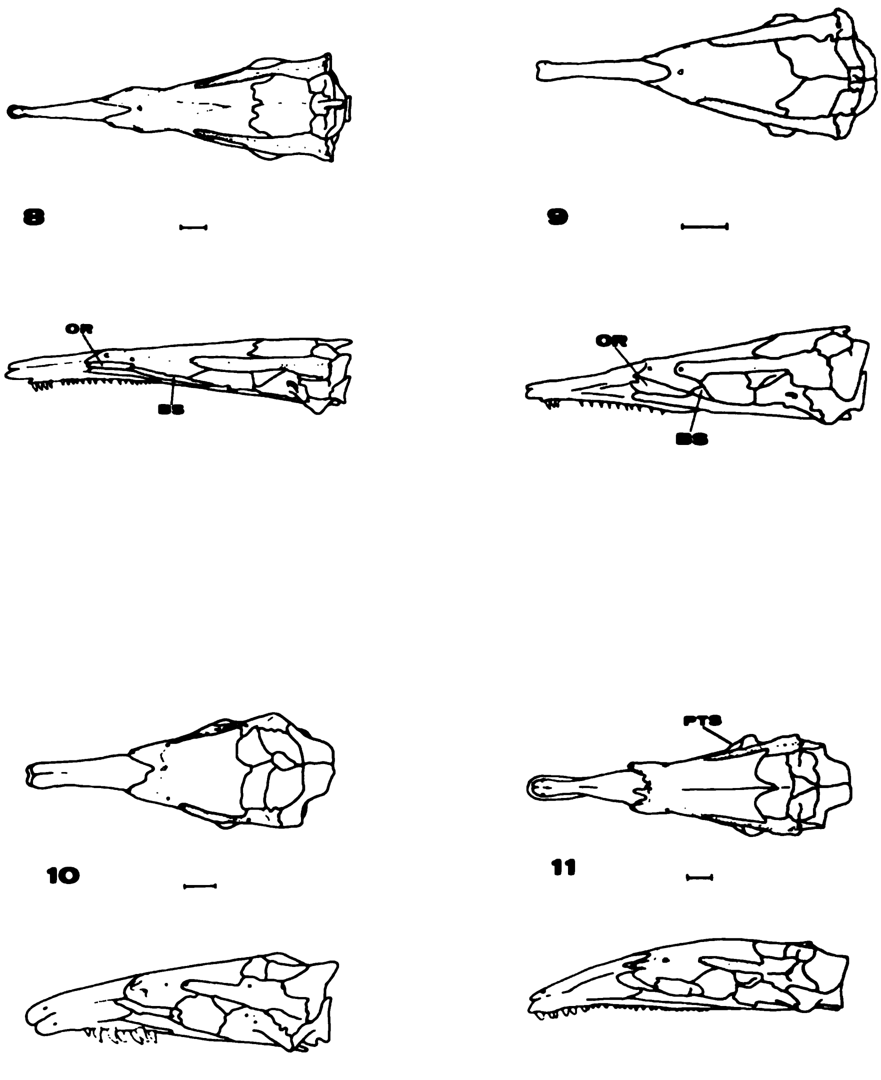


Figure 8. Neurocranium of *Ichthyapus selachops*, SIO 65-232. Scale represents 1 mm. Abbreviations are: BS, basisphenoid; OR, orbit.

Figure 9. Neurocranium of *Stictorhinus potamius*, MZUSP 8959. Scale represents 1 mm Abbreviations are: BS, basisphenoid; OR, orbit.

Figure 10. Neurocranium of *Bascanichthys panamensis*, SIO 71-224. Scale represent 1 mm.

Figure 11. Neurocranium of *Myrichthys xystrurus*, SIO 65-335. Scale represents 1 mm Abbreviation PTS is for pterosphenoid.

s (extremely so in *Benthenchelys*, fig.
oothed in all genera except *Aprognath-*
narrows posteriorly to become the
ich is toothed in most ophichthids
are *Schultzidia*, *Phyllophichthus*,
and *Leuropharus*). The premaxillary
oid dentition, here termed intermaxil-
ntinuous with that of the vomer in *O.*
A gap separates the intermaxillary and
dentition of many ophichthid genera,
rs to be a useful character to indicate
p (table 1). The vomerine dentition
continue onto the parasphenoid. The
ortion forms the anterior margin of the
the medial margin of the nasals. The
perforated anterolaterally by the lat-
issure of the first cranial nerve.
The nasals of *O. zophochir* are paired,
nar, and cartilaginous along their ex-
es. The anterior portion of the supra-
phalic lateralis nerve tract passes
e canal along the median edge of the
nasals of the Myrophinae are either
us or absent. Nasal development
Ophichthinae is variable. In certain
ophichthines (including *Brachysomo-*
lichthys, and *Aplatophis*) the nasals are
mentary or absent. Nasal cartilage ex-
the anterior edge of the PEV; its de-
is quite variable, generally consisting
ort lateral rods; in certain genera it is
rally.
enoid. The parasphenoid (PAS) is a
w, toothless bone, anteriorly overlying
and forming the ventral margin of
rally, it is spread laterally to form the
oor of the cranium, narrows posteri-
splits into two short prongs. It forms
margin of the orbit, and borders the
noid, pterosphenoid, prootic, and
al.
The paired prootics (PRO) combine
paired basioccipitals and pterotics to
otic bulla. They are small, nearly rec-
nd highly perforated with numerous
for the passage of nerves and blood
rough the most conspicuous foramen
hyomandibular trunk of the facial
. Smaller foramina exist for the pas-
e orbital artery and the jugular vein.
axis of the PRO is horizontal. The
ordered by the parasphenoid medially,
phenoid anteriorly, the sphenotic an-
y, the pterotic dorsolaterally, and the
al posteriorly.

Basioccipital. The median basioccipital (BO) is a small, irregularly shaped bone which forms the posterior portion of the otic bulla. Its major axis, in contrast to the prootics, is vertical. It is bordered medially by the parasphenoid, anteriorly by the prootics, and dorsally by the pterotics and exoccipitals.

Pterotic. The paired pterotics (PT) are elongate, narrow anteriorly, and broadly flared laterally and posteriorly, forming the lateral edge of the roof of the cranium. The cephalic lateralis nerve tract passes through the PT and opens anteriorly in the frontal and posteriorly at the posterior PT margin. Anteromedially the PT are bordered by the frontal, followed medially by the parietals and epiotics, anterolaterally by the pterosphenoid and sphenotic, ventrolaterally by the prootic and basioccipital, and posteriorly by the exoccipitals. Posterior to the sphenotics, the PT forms a sheet-like eave extending beyond the body of the cranium.

Exoccipital. The paired exoccipitals (EX) form the dorsal and lateral margins of the foramen magnum. They are sutured along their dorsal midline, and extend posterodorsally and laterally as a semicircular sleeve around the foramen magnum. Ventrally, they contact the basioccipital, and dorsally the supraoccipital. The foramen of the tenth cranial nerve opens posteriorly along the ventral EX-BO border, with the ninth opening lateroventrally from a foramen slightly anterolateral to that of the tenth.

Supraoccipital. The supraoccipital (SO) is single, small, square to subrectangular in shape, and lies along the posterodorsal cranial midline. In *O. zophochir* the narrow median crest of the SO extends posteriorly as a small point. The condition is typical of many ophichthids, although in certain generic groups, particularly *Callechelys* and related genera, they are rounded along the posterior SO margin. The SO extends anteriorly beneath the parietals, and is bordered laterally by the epiotics, posteriorly by the exoccipitals, and anteriorly by the prootics in most genera. In *Schultzidia* the SO has surfaced and has separated the parietals, extending anteriorly to contact the frontal.

Epiotic. The epiotics (EO) are paired, thin, and subrectangular. In *O. zophochir* they are bordered anteriorly by the parietals, laterally by the pterotics, and medially by the supraoccipital. Posteriorly their major axis is changed from horizontal to vertical in forming the dorsolateral margin of the posterior cranial face bordering the exoccipitals. The EO, like the supraoccipital and

the pterotics, forms a narrow sheet-like eave along their posterior margins.

Parietal. The paired, thin, subrectangular parietals (PA) overlay the posterior margin of the frontal. They are bordered anteriorly by the frontal, laterally by the pterotics, posterolaterally by the epiotics, posteriorly by the supraoccipital, and fused medially. In certain ophichthids which have a prominent supraoccipital crest the median ridge development begins along the parietal midline and gradually increases to its posterior projection. Castle (1972: fig. 10) has erred in illustrating the PA of *Benthenchelys* as contacting the sphenotic; in no ophichthid did I find this juncture.

Frontal. The frontal (F) is a single long element which, along with the epiotics and parietals, forms the roof of the cranium. Ontogenetically, the frontal is presumably formed from the fusion of paried lateral elements, but in juveniles and adults there is no evident suture. In *O. zophochir* the F is ridged posteriorly along the dorsal midline. In *Aplatophis* this ridge is developed as a sharp crest. Several nerve tracts pass through the F, including the anterior tract of the cephalic lateralis nerve and the transverse frontal commissure, which is unique to the Ophichthidae. The frontal is deeply split anteriorly by the insertion of the ethmoid portion of the PEV in some genera, and bordered anteroventrally by the orbit and orbitosphenoid, ventrolaterally by the parasphenoid, laterally by the pterotic, and posteriorly by the parietals. The dorsalmost postorbital of certain species of *Ophichthus*, *Echiophis*, and *Brachysomophis* is weakly sutured to the frontal at the level of the transverse commissure.

Basisphenoid (orbitosphenoid of others). The basisphenoid (BS) is a small, unpaired median bone with two lateral wings which forms the posteroventral margin of the orbit. It is bordered dorsally by the frontal, posteriorly by the pterosphenoids, and ventrally is supported by the parasphenoid (a myodome is not present). The BS in certain genera with elongate and depressed neurocrania has become narrow and elongate, as can be seen in a comparison of *Ophichthus* (fig. 2), *Ichthyapus* (fig. 8), and *Stictorhinus* (fig. 9).

Robins (1971: 164-165) has noted that the use of the term "orbitosphenoid" in other eel studies (including Gosline, 1950, 1951, 1952; Regan, 1912; Robins and Robins, 1967; Trewavas, 1932; and others) actually pertained to the BS. Chabanaud (1936) stated that the teleostean BS is not homologous with that of higher vert proposed the name "porpitual" for t teleosts. Springer (1968: 43-44) a Chabanaud's conclusions but conser "basisphenoid" because of its wid in ichthyology, an act with whi

Pterosphenoid (=alisphenoid). Th pterosphenoids (PTS) form the a of the cranium. In *O. zophoch* cave, turning evenly from a l (along the margin of the fron transverse axis which abuts the of the sphenotic. They are bo by the frontal, dorsally by the teriorly by the prootic and sph ally by the parasphenoid. The c men along the PTS-pterotic bo terior opening of the trigemino-f

Otoliths. Ophichthid otoliths, most anguilliforms, are small, a received little attention either on a comparative basis. Studies are l of Frost (1926), which included illu sagittae of *Myrus vulgaris* (=Ech *Ophichthus gomesii*, and *Pisodo* and the photograph of the sagitt *lepturus* in Kotthaus (1968). The of the three otolith pairs) of twel species were compared in this study cus and lapillus were too small to parative value. Ophichthid otoliths a biconvex, with a shallow sulcus on surface. They are particularly distinct a shallow ostial channel which ope rather than turning dorsally and op the sulcus, as is typical of the Congrid zel and Lamber, 1962: fig. A; Frost, 10-11, 15). The sagittae of *Ophisuru ichthus* (fig. 12) possess a short ante and are more elongate than those of and *Myrophis*, which are roughly cir tae of *Myrichthys* and *Echiophis* are i in shape.

Dentition. Dentition has often bee principal character to define and ophichthid genera. The location an teeth was found in this study to be a indication of relationship. The denti *zophochir* represents the generalized condition in being multiserial, conic all tooth bearing bones (vomer, eth maxilla, maxilla, and dentary). Consid ation exists within the family, inc elongate fanglike dentition of *Apla* molariform or granular dentition of

Figure 12. Otoliths (medial face, left sagitta) of several ophichthid species. Anterior end up. Sulcus outline inked in. Scale represents 2 mm.

A. *Ophichthus triserialis*
B. *Ophichthus zophochir*
C. *Ophisurus serpens*
D. *Echiophis intertinctus*
E. *Ethadophis merenda* (orientation uncertain)
F. *Myrichthys xystrurus*
G. *Echelus pachyrhynchus*
H. *Aplatophis chauliodus*
I. *Myrophis vafer*

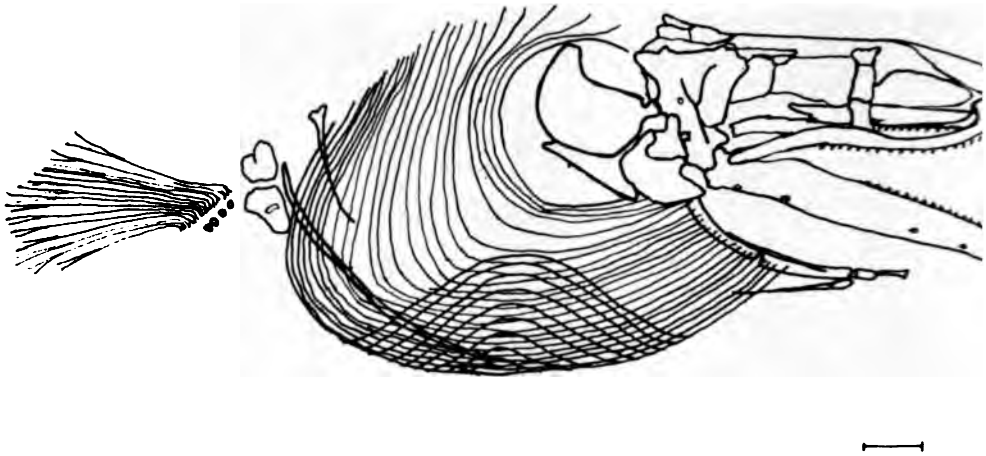


Figure 13. Head skeleton of *Ophichthus zophochir*, SIO 60-304. Scale represents Refer to Figures 2-3 (neurocranium), 14 (suspensorium), 17 (hyoid), and 19 (pectoral for names of bones.

Pisodonophis and certain species of *Muraenichthys*, the minute, nearly villiform dentition of *Schultzidia*, and the smooth toothless vomer of *Leiuranus, Leuropharus, Phyllophichthus* and *Schultzidia*. Characteristics of the dentition of ophichthid genera are summarized in table 1.

Suspensorium and Jaws

The conditions of the dentition, suspensorium, and jaws are directly related to the feeding habits of the various genera. In ophichthids, differences in feeding habits (e.g., major differences in prey items and adaptations of the predators to the different habitats) are greater between the species of different genera than between congeners. These differences are well evidenced in the form of the suspensorium and jaws of various ophichthids. The juxtaposition of the neurocranium, suspensorium and jaws, pectoral girdle and hyoid apparatus of *O. zophochir* is illustrated in figure 13.

All elements of the suspensorium and jaws are paired.

Hyomandibular. The hyomandibular (HYM) is stout and shaped like an inverted right triangle. The HYM of strong-jawed piscivorous genera is generally strongly ridged for the attachment of the massive adductor mandibularis muscle. The dorsal surface of the HYM abuts the sphenotic and pterotic. A small irregular condyle along the antero-dorsal margin of the HYM fits into a shallow socket formed along the sphenotic-pterotic suture. The large process on the posterior HYM margin adjoins the anterior process ercle. The ventral portion of the H the quadrate.

Quadrate. The small, stout quadrate sutured to the HYM. The vertical rid outer face of the HYM is continuo Q. Ventrally the Q bears a broad r cave process that contacts the artic the mandible.

Articular. The wedge-shaped artic narrowed anteriorly, and slides int within the dentary. A remnant of meckelian is present along the inner AR of *O. zophochir;* its presence in was not systematically determined. a grooved socket in the AR meets socket of the quadrate.

Dentary. The dentary (D) is the to of the mandible, joined by the a teriorly and adjoining its opposite me symphysis by a cartilaginous connecti

Postorbitals. The three postorbita most ophichthids are separate, weak surround the nerve tract connecting orbital and infraorbital pore tracts. *O. zophochir* however, are speciali largement and fusion to form a cont bracing the mandible and neurocr specialization, also present in other *Ophichthus* and *Echiophis*, is extrem *somophis* (fig. 15).

The antorbital cartilaginous strut line (1952) described for *Echelus my*

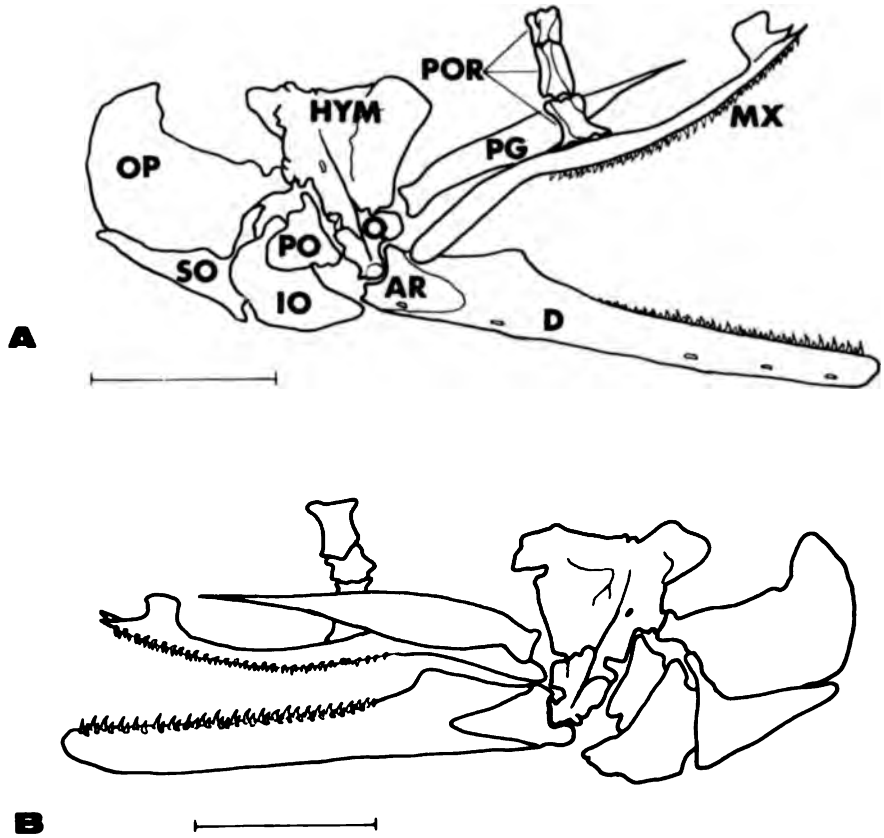


Figure 14. Suspensorium and jaws of *Ophichthus zophochir*, SIO 65-166. Scale represents 5 mm. Abbreviations are: AR, articular; D, dentary; HYM, hyomandibular; IO, interopercle; MX, maxilla; OP, opercle; PG, pterygoid; PO, preopercle; POR, postorbitals; Q, quadrate; SOP, subopercle.

A. Outer face

B. Inner face

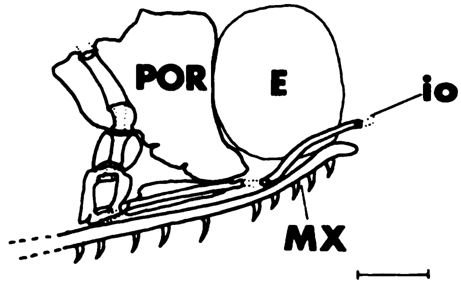


Figure 15. Right postorbital series of *Brachysomophis sauropsis*. Scale represents 1 Abbreviations are: E, eyeball; MX, maxilla; POR, dorsal-most postorbital; io, infrac pore tract.

found in other ophichthids studied (see Remarks on *Echelus)*. A similar cartilaginous strut has been observed in other eels however, including the dysommid *Atractodenchelys phrix* and in the Synaphorbranchidae (Robins and Robins, 1970: 307). They felt "it (probably) represents either the prefrontal or lateral ethmoid or their fusion."

Pterygoid (=palatopterygoid). Pterygoid (PG) development is variable within the family, although a clear pattern of relationship was not apparent. The PG is reduced to a narrow splint in most ophichthids. In *O. zophochir* it is thin, laminar, pointed anteriorly, and blunt posteriorly. It is held in place by the dermal layer and connective tissue, and contacts neither the quadrate nor the hyomandibular. The PG of all ophichthids tapers anteriorly, and often posteriorly, is largely cartilaginous in many species, and does not appear to serve any distinct purpose. *Ahlia* is exceptional in differing from the closely related species of *Myrophis* in the shape of its PG and in lacking vomerine teeth (fig. 30). A true palatine is not present in ophichthids, as shown by Robins and Robins (1971) in their discussion of the "palatopterygoid arcade."

Maxilla. The maxilla (MX) of all ophichthids is toothed, elongate, and possesses an anterior dorsal process which articulates with the PEV. Posteriorly, the maxillae of *O. zophochir* are truncate and do not extend beyond the articular. The generalized ophichthid condition however, is that of a toothless, elongate, ossifi aginous extension of the MX beyond to the articular. The location of maxill tion with the vomer is affected by the of the snout and jaw, and is quite var the family. The condition is certain genera is illustrated in figures 16 and

In concluding this section on the ium and suspensorium and jaws, c ments are in order relating to their tions and functional anatomy. Typical civorous adaptations of species of *Brachysomophis, Echiophis* and rela are the strengthening provided by vault, the elongate pterotics, the bro of the hyomandibular along the ne and the bracing of the maxillae to th means of the fused postorbitals. Ar condition exists in the muraenid gen *thorax*, in which a postorbital strut the jaws and suspensorium (cf. Bu fig. 6). Other ophichthid genera, among the Myrophinae and elong thines, are adapted to diets of min brate prey, and have extremely redu crania, suspensoria, jaws, and dentiti

Opercular Series

The opercular series of ophichthi anguilliforms in general, is greatly re reduction is apparently related to t

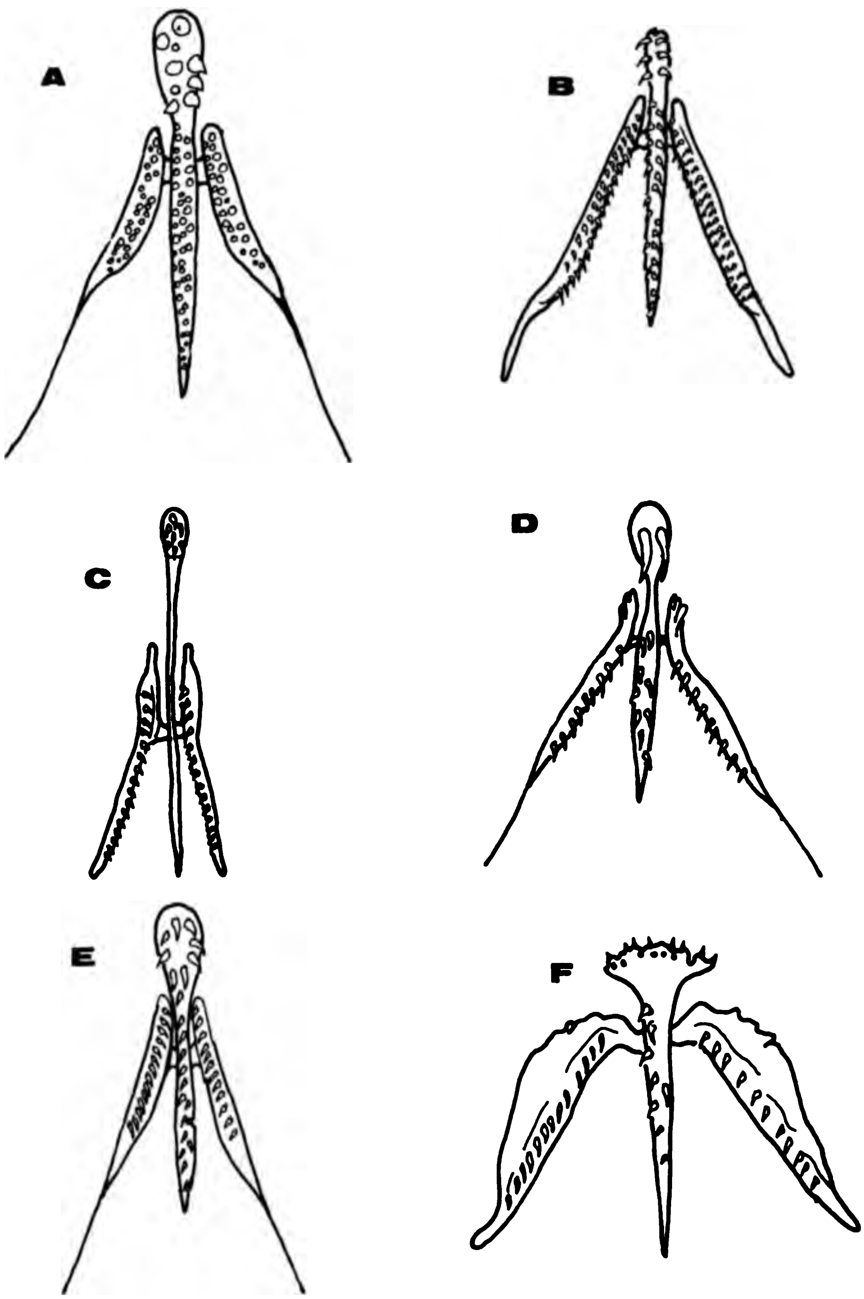


Figure 16. Maxillary-vomer apposition of several ophichthids. *Benthenchelys cartieri* enlarged 20 times, all others 9 times.

A. *Myrichthys xystrurus*
B. *Ophichthus zophochir*
C. *Phyllophichthus xenodontus*
D. *Callechelys marmoratus*
E. *Muraenichthys chilensis*
F. *Benthenchelys cartieri*

in number and importance of the branchiostegal rays as supporting elements for the branchial cavity (Greenwood, et al., 1966). Gosline (1959) has correlated the reduction of the opercular series, posterior displacement of the gill arches and pectoral girdle, and the separation of the pectoral girdle from the neurocranium with the peculiar branchial pump and circulatory mechanism of anguilliforms. Opercular reduction and deossification of cartilage, and the increase in the number of branchiostegals of ophichthids appear to be greatest in the smaller myrophines and elongate bascanichthyins and sphagebranchins. Within the Ophichthidae, the condition of *O. zophochir* closely approximates the generalized (primitive) state (fig. 14). The opercle (OP), the largest of the series, is posterior to the hyomandibular and above the subopercle (SOP), with its ventral margin lying lateral to the dorsal margin of the SOP. The interopercle (IO) overlays the SOP and is below the OP. The preopercle (PO), smallest of the series, overlays the (IO) and contains the tract of the preoperculomandibular nerve. The SOP and IO are the least ossified of the series, although the distal margins of most members of the opercular series are cartilaginous in most ophichthids.

Several specializations in each subfamily are useful indicators of phylogeny. For example, the SOP is produced posteriorly as a projection enclosing the ventral and posterior margins of the OP in species of *Myrophis* (fig. 33), *Ahlia, Muraenichthys (*Gosline, 1951a: fig. 3), *Pseudomyrophis*, and *Schismorhynchus*. This SOP-OP morphology is typical of other eel families, including certain Congridae (Asano, 1962; Rosenblatt, 1967), Moringuidae (Trewavas, 1932; Smith and Castle, 1972), Xenocongridae (Gosline, 1950, 1951b; Robins and Robins, 1967), and *Xenomystax atrarius* (Peden, 1972). The opercular series of *Callechelys* and related genera is reduced and has a conspicuously fringed appearance along the margin. The opercular series of *Stictorhinus, Apterichtus, Ichthyapus*, and related genera are quite reduced, with elements absent in certain genera.

Hyoid Apparatus

The hyoid apparatus and the associated branchiostegals provide fundamental characters which help to unify the subfamilies within the Ophichthidae. In particular, the broad overlap along the ventral midline of the branchial basket is herein considered a major phylogenetic character of the family, not evidenced by homology o
ence in other eel families. The importa
character, which later led to the coi
the Neenchelidae, Echelidae (in part
Ophichthidae, was recognized by I
Storey (1939), Gosline (1952), Bertin
bourg (1958), Böhlke (1960) and Nels

The general usage of the term "epih
ichthyological literature has been in
Goodrich (1930: 405-406) has pointe
true epihyal is homologous with the h
ular, and the element incorrectly t
epihyal represents the posterior ossifi
of the ceratohyal. I am in agreement v
rich's conclusions, however in view o
spread usage in ichthyology, I have h
the term "epihyal" to represent the p
the two ceratohyal elements, and the t
tohyal" for the anterior element.

The following description of the hyo
tus is based on that of *O. zophochir*
The apparatus consists of the unpaired
(GH) and urohyal (UH), and paired up
hyals (HH), ceratohyals (CH), and epih
The interhyal is absent. The outer pos
margin of the EH is connected by ca
the inner face of the quadrate and pro
port for the branchial basket. The CH
are connected by a stout cartilaginous
fording little flexibility along the arc
strengthening is provided by the flank
like posterior extension of the CH
outer edge of the EH. The GH is groo
the posterodorsal half and extends for
small cylindrical teat. The GH and pai
HH are interconnected by a weak ca
plate. The upper HH is fused along a
slightly flexible suture to the CH. A ve
extension of the CH braces the HH.
lying ventrad to the HH, GH and CH, i
anteriorly and has a short cartilaginou
nection from its anterior midpoint to
ventral margin of the GH. Posteriorly
extends as a slender ossified spike s
by a membranous sheath and ove
branchiostegal rays. All the branchios
are inserted on the external face of t
on the CH, 1 on the cartilaginous inter
19 on the EH. The inner 3 and outer
closely grouped basally and the rema
more widely spaced. Rays 6-16 are
slightly at their bases but filiform fo
mainder of their length. The rays broad
along the ventral midline in a characte
ner. The distal 19 rays of the left EH

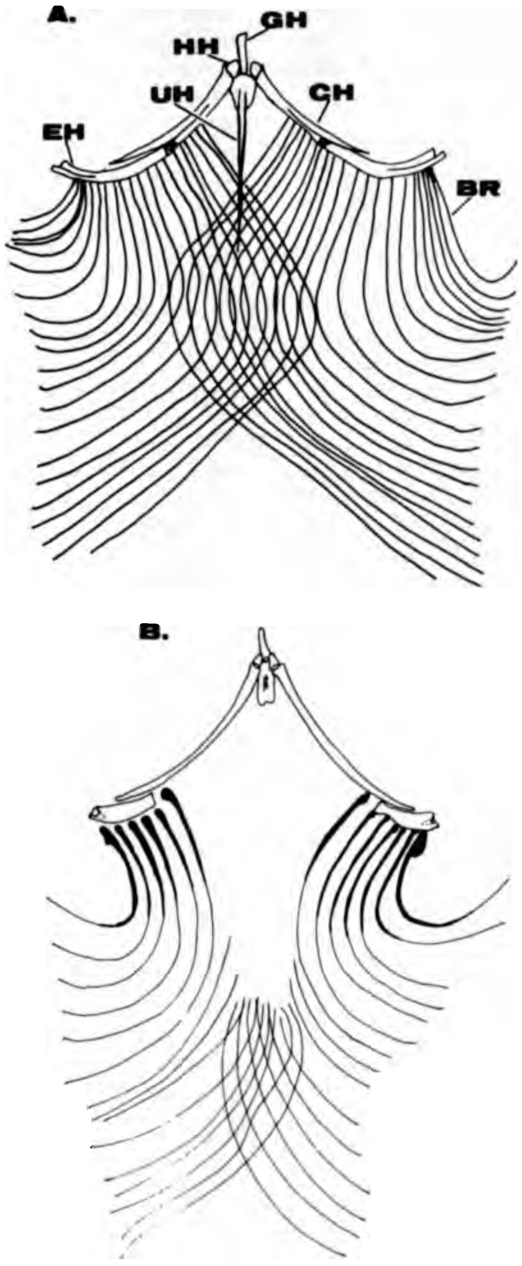


Figure 17. Hyoid arch and branchiostegals of *Ophichthus zophochir*, an ophichthine, and *Muraenichthys chilensis*, a myrophine. Dorsal view. Scale represents 1 mm. Abbreviations are: BR, branchiostegal rays; CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyal; UH, urohyal.

A. *Ophichthus zophochir*

B. *Muraenichthys chilensis* (posterior-most branchiostegals not illustrated)

aginous interspace are overlain by all the rays of the right arch, which are in turn overlain by the remaining left CH rays. This pattern of the left CH rays overlaying the right CH and EH rays which overlap the left EH rays is consistent within the Ophichthidae.

The location and number of branchiostegal rays among the genera of ophichthids (table 2) and the proximity of the branchiostegal rays to the hyoid arch differs markedly in the ophichthid subfamilies. In the Myrophinae, which appear to follow the generalized anguilliform condition, the branchiostegal rays are attached to the outer face of the EH, often with a single ray on the CH (fig. 17B, *Muraenichthys*). The remainder of the branchiostegal rays, which will hereafter be referred to as the "accessory branchiostegal rays", are unattached and basally lie well behind the hyoid arch. In the Myrophinae, these vary from as many as 13 pairs in *Benthenchelys cartieri* to 42 pairs in *Myrophis vafer*. In the Ophichthinae, all branchiostegal rays are attached to the outer face of the hyoid arch(fig. 17A, *Ophichthus*), although in some species the rays have secondarily become detached.

The extreme development of this branchiostegal apparatus is obviously a means of strengthening the gill basket. The manner in which several ophichthines, particularly *Ophichthus*, *Echiophis*, *Brachysomophis*, and *Aplatophis* have all the rays attached to the face of the hyoid is probably related to a diet of struggling prey, in contrast to the myrophine condition of free rays and their diet of comparatively weak prey. The reduction of the opercular apparatus and the posterior displacement of the entire gill arch complex necessitates a supplementary skeletal framework to prevent the gill basket from collapsing during the normal burrowing activities of ophichthids. The posterior displacement of the gill arches among anguilliform families is extreme in the Ophichthidae and the Moringuidae (see Nelson, 1966a: fig. 58), both of which comprise predominantly sand and mud-burrowing forms.

The accessory branchiostegal apparatus of ophichthid and echelid eels was recognized by earlier workers, but Parr (1930) was the first to describe it and suggest its function. He created the term "jugostegalia" for the accessory skeleton of the gill cover in species of *Myrophis*. Because of their number he did not consider the attached rays to be homologous with the branchiostegals. In that the accessory rays are undifferentiable from the branchiostegal rays, especially in those ophichthine species in which all rays are attached to the hyoid, I prefe Parr's term, jugostegalia. Problems c consideration of jugostegalia as a s tity, even if one assumes them to be with the branchiostegals. For exampl ing Parr's concept of jugostegalia a which are free from the hyoid, McAl 85) stated that "*Myrichthys* (has) 2 stegal rays) plus 4 jugostegalia... plus 34-36 jugostegalia." McAllister's tention of the term jugostegalia "fo ondarily multiplied, overlapping and chiostegals found in certain anguillif adequate as seen in the above usage. propose that a more flexible termino plied to those rays, and prefer the te sory branchiostegal rays".

The branchiostegal rays also refle eric and intergeneric similarities th basal thickening and secondary mu The outermost rays of all myrophines ophichthines are proximally broad *Muraenichthys*, fig. 17B, and *Neenchel* 1966b: fig. 2a). This condition is sir general anguilliform condition as di congrids, muraenids, anguillids, and o families. In other ophichthines, particu *chthus*, *Aplatophis*, *Myrichthys*, and *mus*, the branchiostegals are filiform t The basal splitting or secondary multi the few inner and outermost rays i secondarily related to the number and the rays along the arch. For example, of *Echiophis* and *Ophisurus* the bra on the CH are paired, and are ofte their bases. No trends were apparent dition within the Ophichthidae, henc to be of limited value as a phylog cator.

The urohyal of most ophichthines i posteriorly as an ossified spike. The myrophines is limited to an ossified with cartilaginous posterior filament ophichthines that lack the ossified clearly derived from the generalize typified by *Ophichthus*, rather tha somewhat similar myrophine conditi sory survey of other eel families in the ophichthine condition is primitive to the more specialized myrophine c

A major subfamilial difference i denced in the ceratohyal. Without ex CH of the Ophichthinae is split into and pointed distal portion and a short medial portion which connects, by

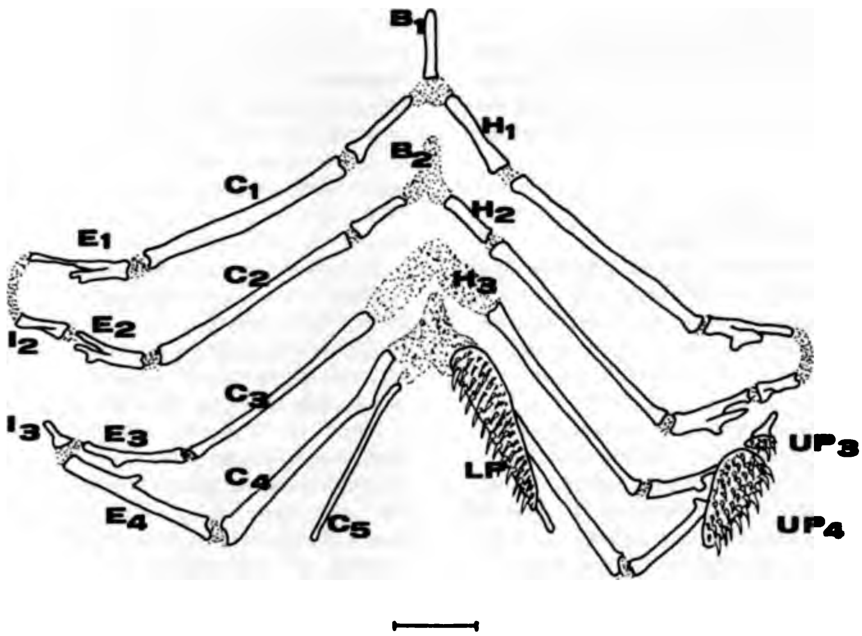


Figure 18. Gill arch skeleton of *Ophichthus zophochir*, SIO 65-166. Dorsal view. Gill arches have been cut along the dorsal midline and spread laterally; left upper and lower pharyngeal tooth plates are removed to show underlying bones. Stippling indicates cartilage. Scale represents 1 mm. Abbreviations are: B_1, first basibranchial; C_1, first ceratobranchial; E_1, first epibranchial; H_1, first hypobranchial; I_2, second infrapharyngobranchial; LP, lower pharyngeal tooth plate; UP_3, upper pharyngeal tooth plate.

cartilage, with the EH (fig. 17A). The myrophine CH is not split, but is rather a simple bowed bone, distal to, and terminating at about the midpoint, of the EH. The myrophine condition appears to involve a unique reduction, whereas the ophichthine condition is similar to that of the Congridae (Asano, 1962; D. Smith, 1971; Rosenblatt, 1967) and other eel families.

The hypohyals of most ophichthines are like those of *O. zophochir*. In certain otherwise dissimilar genera, including *Schismorhynchus, Aprognathodon*, and *Phyllophichthus*, the HH are absent. Careful examination of the anterior end of the CH did not reveal a suture or line of fusion, so it might be assumed that the HH are lost altogether. Observation of an ontogenetic series might provide proof of fusion or absence.

Gill Arches

Certain elements of the anguilliform gill arch skeleton have been shown to be important indicators of phylogeny (Nelson, 1966a). The Ophichthidae differ from all other eel families in a combination of gill arch characters, including: a cartilaginous connection between the proximal ends of the dorsal part of the first and second gill arches (according to Nelson, peculiar to the Ophichthidae); first basibranchial either ossified or absent, all others cartilaginous, rudimentary, or absent; hypobranchials 1-2 ossified; second infrapharyngobranchial (I_3) ossified. If one considers the anguillid or congrid gill arch conditions, that of numerous ossified elements with minor loss or reduction, to be primitive among the anguilliforms, then the ophichthids are considerably advanced in having several osseus elements replaced with cartilage, and in having others reduced or entirely lost. Extending this supposition within the Ophichthidae, the Ophichthinae, and in particular the Ophichthini, are more primitive than the Myrophinae, which have lost the fifth ceratobranchial (C_5) and have reduced or lost certain basibranchials (tables 3-4). The ophichthids are also specialized in having the gill arch skeleton displaced posteriorly in relation to the cranium. Among shallow-water eel families this condition is exceeded only in the Moringuidae (see Nelson, 1966a: fig. 58). References to gill arches of ophichthid species are limited to Popta's (1904) pioneering study of apodal gill arches (which treated *Muraenichthys gymnopterus, Leiuranus semicinctus, Caecula polyophthalmus, Pisodonophis boro*, and *Myrichthys colubrinus*), Nelson's (1966a) detailed study, which included species from 1 thid genera, and Nelson's (1966b) tre *Neenchelys buitendijki*.

The following description of the gil tem of *Ophichthus zophochir* (fig. 18) the presumably primitive condition Ophichthidae. Terminology of gill arc follows that of Nelson (1969: 480). branchials are single elements, not nected, lying along the ventral midlin gill arch elements are paired. The firs chial is ossified, slender, and connecte age to the first hypobranchials. Basibra are cartilaginous and connected to th hypobranchial pair. Hypobranchials 1- fied and stout. Hypobranchials 3-5 a nous, with 4 and 5 fused. Ceratobra are ossified and subequal. Ceratobra reduced to a slender filament which i most of its length with the ventral sur ventral pharyngeal tooth plate. Epibra are short, stout, and bear various pr cartilaginous or ligamentous attachmer infrapharyngobranchial (I_1), as in all sent. The second connects to the first ial by a cartilaginous strap; this co mentioned earlier, is peculiar to all o The third is "T" shaped and distally s third upper pharyngeal tooth plate upper pharyngeal plates are separate ture, the third being much smalle fourth (UP_4). Each plate bears along a single row of slightly retrorse co which grades to a fine-toothed pavem the tooth plates overlie each other, ar the esophageal canal so that the co toothed areas of the upper and lowe aligned.

The third hypobranchial is cartil nearly all ophichthids. This specializ ably functions to increase the flexib gill arch skeleton and, in particula further anterior movement of the low geal tooth plates. For the same reason hypobranchial is never ossified. The s ossified third hypobranchials, *Dalophi Aprognathodon platyventris*, and *Elaps hinus*, are highly specialized and not lated. Two examples of each of the species were examined to rule out the of anomalous specimens. Both spe *Elapsopis* had a well ossified H_3 slender, nearly subequal tooth plat conical biserial teeth. The two sp *Aprognathodon* were somewhat aber

. In one, the left H_3 was well ossi- right was cartilaginous. The other liscontinuous pieces of bone lying tilaginous matrix on both sides. In ens the short, stout H_{1-4} pairs nearly he ventral midline, and the small bore several slender pointed teeth. eptional species there has probably n to an ossified H_3 condition rather tion of the primitive ancestral oph- ition, possibly related to a special- ich would require less flexibility in ikeleton.

c examination and interpretation of elements is often difficult, particu- entiating the rudimentary and cartil- litions of the basibranchials. Nelson for example, considered the fourth condition of *Leiuranus semicinctus* *enchelys phoenixensis* to differ, al- authors have regarded the latter color variant synonymous with the s. The interpretation of the UP_3-UP_4 tends to be subjective and is not l upon. Since anomalies often occur arch skeleton, duplicate specimens ed in this study when suspicious re- countered.

966a) identified certain ophichthid he basis of the gill arch conditions. ised (a) those genera with a moder- veloped series of basibranchials and ifth ceratobranchial, (b) those with or cartilaginous, and (c) those with basibranchials and lacking C_5, i.e., nae. Nelson erred in considering 's to be an echeline (=myrophine) gnize the generalized condition of hials and C_5. My study has shown ct in his other interpretations and other genera within his general

onal significance of the modification ches in apodal fishes was discussed 1966a). The posterior displacement hes, the reduction and modification ments, and the absence of a firm on with the cranium has trans- function from prey catching (now aws and cranium alone) to one of food items through a secondarily harynx. As Nelson (p. 404) has "many of these same modifications d independently among syngnathi- nd symbranchiform fishes . . ., possibly also as a result of spatial separation of jaws and gill arches."

Pectoral Girdle

The pectoral girdle varies considerably within the Ophichthidae, grading from a well developed to a reduced condition in both subfamilies. The primitive condition, represented by *Ophichthus* (fig. 19A) in the Ophichthinae and by *Myrophis* in the Myrophinae (figs. 20E-F), includes the retention of the cleithrum (Cl), supracleithrum (SCl), scapula (=hypercoracoid) (Sc), and coracoid (=hypocoracoid) (Co), and in the Ophichthinae, the actinosts. The postemporal is absent and the pectoral girdle is not attached to the cranium in anguilliforms (Gosline, 1971). The pectoral fin is best developed in genera such as *Ophichthus, Echelus, Echiophis, Mystriophis, Aplatophis, Malvoliophis, Cirrhimuraena, Pisodonophis,* and *Pogonophis* in the Ophichthinae, and *Myrophis* and *Ahlia* in the Myrophinae. The pectoral fin rays are in some cases *(Ahlia* and *Myrophis)* multiply-branched. Pectoral rays vary in number from three to four weak stubs in *Bascanichthys panamensis* to 18 rays in *Pogonophis fossatus*.

The coracoid and scapula generally lie within a cartilaginous plate which provides a rigid support for pectoral fin movement. When present, the pectoral fin base lies in a dorsoventral plane and is broad-based in relation to the fin length (extremely so in *Myrichthys),* offering little rotational movement. Observations of live *Echiophis* sp. and *Ophichthus triserialis* indicate that those ophichthines use their pectoral fins to assist the body musculature in making short darting movements during feeding. Observations of live *Bascanichthys panamensis* suggest that the highly reduced pectoral fin serves little, if any, locomotory function. In those forms lacking pectoral fins, the cartilage, as well as the Co and Sc, is reduced or absent entirely. The trend in pectoral girdle reduction is related to the burrowing habit of many ophichthids. The primary function of the pectoral girdle as the structural support for the pectoral fin has in burrowing forms become one of structural support for the posterior end of the branchial basket. In no species are all girdle elements absent, but in *Cirricaecula* (fig. 19N) and in species of *Ichthyapus* only the Cl remains, and in species of *Muraenichthys* the Cl is a thin curved bone which is nearly identical in appearance and in function to the last of the accessory branchiostegals. The SCl of several

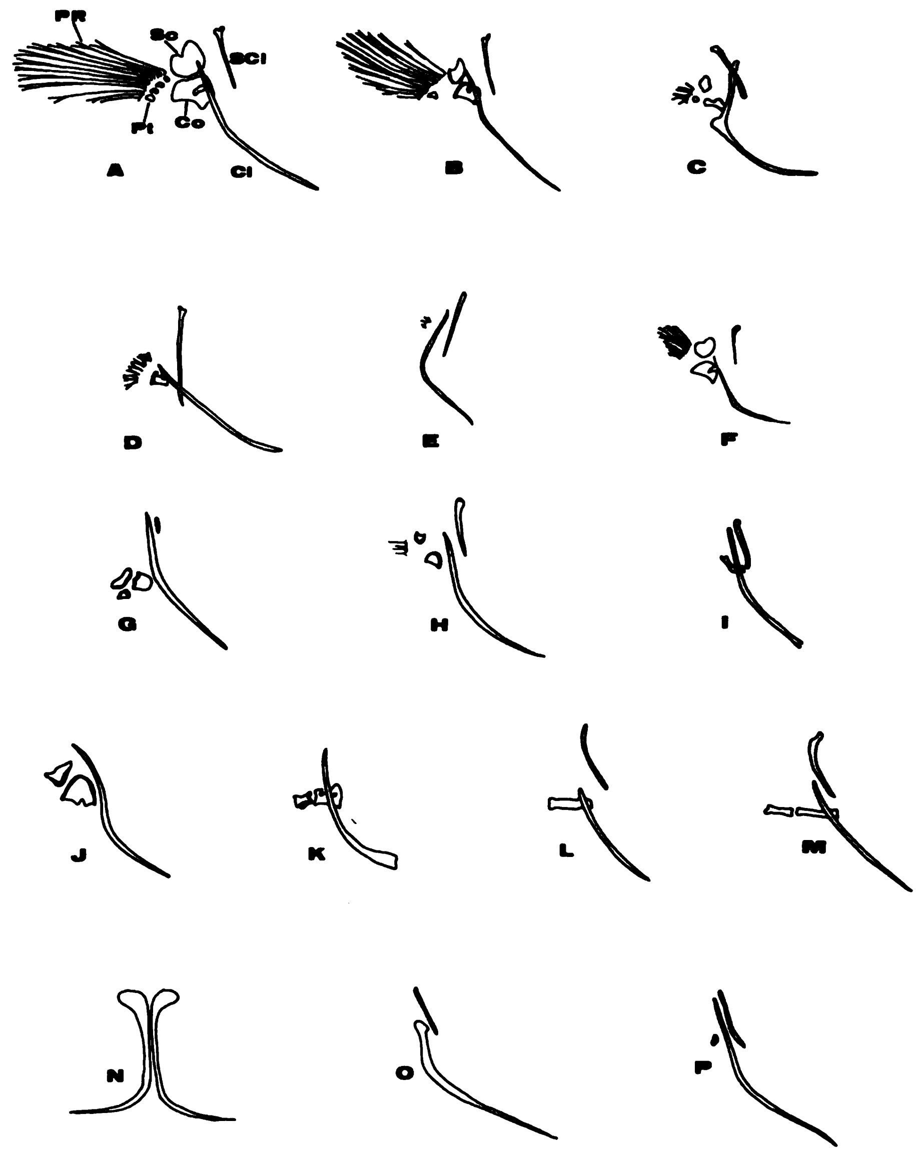


Figure 19. Pectoral girdle of various representative ophichthine genera. All are shown in lateral view, right side, except *Cirricaecula* which is viewed ventrally. Abbreviations are Cl, cleithrum; Co, coracoid; PR, pectoral rays; Pt, pterygiophores; Sc, scapula; SCl, supracleithrum.

A. *Ophichthus zophochir*
B. *Pisodonophis boro*
C. *Elapsopis cyclorhinus*
D. *Myrichthys xystrurus*
E. *Quassiremus nothochir*
F. *Aplatophis chauliodus*
G. *Caralophia loxochila*
H. *Bascanichthys panamensis*
I. *Phaenomonas pinnata*
J. *Caecula pterygera*
K. *Lamnostoma orientalis*
L. *Callechelys marmoratus*
M. *Aprognathodon platyventris*
N. *Cirricaecula johnsoni*
O. *Apterichtus flavicaudus*
P. *Yirrkala tenuis*

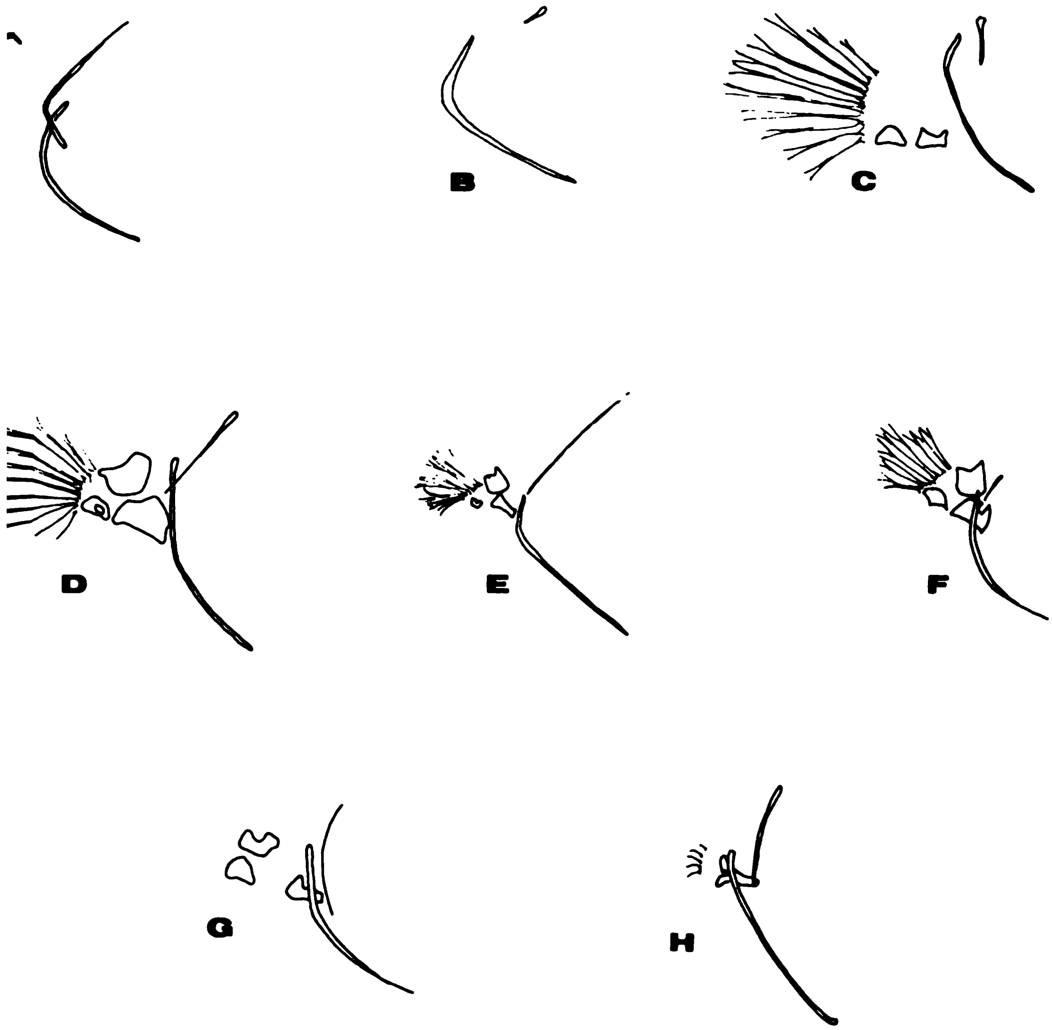


Figure 20. Pectoral girdle of various representative myrophine genera. All are shown in lateral view, right side.

A. *Muraenichthys gymnopterus*
B. *Muraenichthys chilensis*
C. *Benthenchelys cartieri*
D. *Ahlia egmontis*
E. *Myrophis vafer*
F. *Myrophis uropterus*
G. *Neenchelys buitendijki* (from Nelson, 1966b: fig. 2c), pectoral fin rays not illustrated
H. *Pseudomyrophis micropinna*

species of *Muraenichthys* is merely a thin sliver (e.g., *M. chilensis*, fig. 20B) and it is lost altogether in *Schismorhynchus*.

A peculiar Co and Sc condition exists in the Callechelyini and several of the Bascanichthyini, representing a unique ophichthid specialization which is not seen in other apodal fishes. It is nearly universal among eels for the Sc to be a nearly round bone (flattened slightly on the posterodorsal edge) lying above the Co (also nearly round but slightly flattened on the posteroventral edge), one or both of which are fenestrated. This is also the generalized ophichthine and myrophine condition. The Callechelyini possess either one or two small rod-shaped bones which are connected by cartilage and are oriented horizontally in the normal location of the Co (see *Aprognathodon*, fig. 19M and *Callechelys marmoratus*, fig. 19L). Species of *Phaenomonas* and *Ethadophis*, and the sphagebranchin *Lamnostoma orientalis* are similar in this condition. The homologies of these two rod-shaped bones are not entirely clear, but until further evidence is discovered, I will consider the anterior bone to be homologous with the Co and the posterior one to be homologous with the Sc. Pectoral girdle reduction in *Myrichthys* provides an indictation of its generic homologies, particularly to species of *Pisodonophis*. The Sc in all species of *Myrichthys* is lost and the Co has lost its dorsal curvature (see fig. 19D). This condition is also that of *Pisodonophis daspilotus*, a species clearly more similar to other *Pisodonophis* than to species of *Myrichthys* in other osteological characters. Further similarities in all species of both genera include the shape of the Cl and SCl. Other *Pisodonophis* examined have retained the Sc and a complete Co, a condition more like that of *Ophichthus*.

The ancestral condition of those genera which entirely lack the Co and Sc is not indicated by remnants of cartilage or bone or transitional species, and is therefore indeterminable. The loss of the Co and Sc in *Ichthyapus*, *Apterichtus*, *Cirricaecula* and *Quassiremus* may have been independent, although the first three genera are related on the basis of other characters.

Lateralis System

The apodal lateralis system and associated bones have been shown to be useful indicators of relationship, particularly within the Congridae (Asano, 1962; D. Smith, 1972). Asano showed that the number of pores within the cephalic canal vary within and between gene nese congrids. The lateralis system Ophichthidae was found to differ in a istic manner at the subfamilial and t It is best developed in the Ophichthin duced in the Myrophinae. The ophic alis system has been described and ill several occasions, usually on a species basis and not in a comparative man works include: Allis (1903), *Ophisur* and *Echelus myrus* (as *Myrus vulgari.* (1951a), *Ichthyapus vulturis* (as *Cae rhyncha);* Hopkirk (1965), *Ophichth chir;* Nelson (1966b), *Neenchelys l* Blache (1968), *Echelus myrus, E. pac* and *Myrophis plumbeus;* Blache (197 *phis rostellatus, M. crosnieri,* and *Ec tertinctus;* and Blache and Cadenat (*richthys pardalis, Bascanichthys* spp., *lechelys* spp.

The ophichthid lateralis system is di seven canals: lateral line, supraorbital tal, preoperculomandibular, temporal, poral commissure, and frontal comm canals lie either within certain ceph (frontal, pterotic, nasal, preopercle, and dentary) or weakly ossified tube which are broken at short intervals flexibility. The Ophichthidae are dis having the right and left sides of th lateralis system connected through and temporal canals.

The following description of the la tem of *Ophichthus zophochir*, a spe shows little reduction and minor spe illustrates the general ophichthine cor 21). The supraorbital canal connects infraorbital and temporal series poste with its opposite member dorsally transverse frontal commissure. A sing supraorbital pore is present. Three s pores are associated with the nasal, pore lying within that bone. The a ethmoidal pore is connected to the s canal by a short cartilaginous connec are six infraorbital pores. Four lie b beneath the eye in an ossified canal tally overlying the maxilla, followed by cal pores lying behind the orbit and to a canal passing through the three bones. The supraorbital canal conne orly with the temporal canal and c passing through the frontal and p single median supratemporal pore is erally by a pore on each side. Th

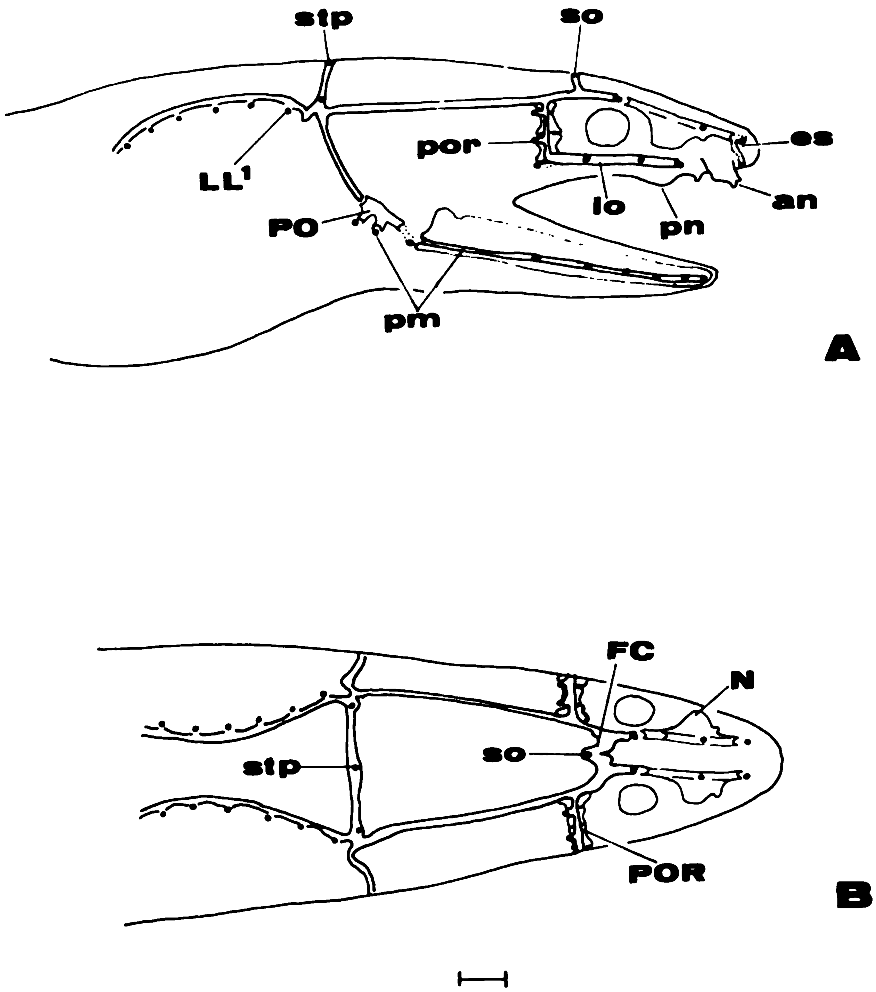


Figure 21. Cephalic lateralis system and associated bones of *Ophichthus zophochir*, SIO 60-309. Stippling indicates cartilaginous canal section. Scale represents 1 mm. Abbreviations are: an, anterior nostril; es, ethmoid section of supraorbital pores; FC, transverse frontal commissure; io, infraorbital pores; LL[1], anteriomost lateral line pore; N, nasal bone; pm, preoperculomandibular pores; pn, location of posterior nostril; PO, preopercle; por, postorbital pores; POR, postorbital bones; so, supraorbital pore; stp, supratemporal pore.

A. Right side view

B. Dorsal view

canal extends posteriorly to the lateral line canal and ventrally to the preoperculomandibular canal. The preopercular section connects by an ossified tube to the preopercle, with two ventrolateral pores passing from the bone. A cartilaginous connection with the third preopercular pore joins the preopercular and mandibular sections. By overlying the quadrate and angular-articular juncture this cartilaginous connection provides the flexibility necessary during jaw movement. The seven pores comprising the mandibular series are unevenly spaced along the dentary. The lateral line (LL) canal extends posteriorly from the preoperculomandibular-temporal canal juncture, loops above the branchial basket, and continues midlaterally to within 0.2 head length of the tail tip. There are approximately 150 LL pores, 51 of them before the anal origin. Lateral line ossicles are moderately ossified, separated at each pore, and open along the distal margin (fig. 22F). On the medial face of all LL ossicles there is a centrally located opening for the nerve. Lateral line ossicle development is reduced posteriorly and absent before the last few caudal pores.

Suprageneric relationships among ophichthid genera are indicated by repeating pore patterns in certain cephalic canals, particularly in the preopercular portion of the preoperculomandibular canal and in the temporal canal (table 5). The generalized ophichthine condition consists of three preopercular pores and a single temporal pore on either side of the median supratemporal pore (as in *Ophichthus zophochir*, Fig 21, and *Ophisurus serpens*, Fig. 24B). The third preopercular pore (pop^3) is lost in certain Ophichthini and all Callechelyini and Bascanichthyini. Certain Sphagebranchini are specialized in having a fourth preopercular pore (pop^4) and a second temporal pore (tp^2), as in *Ichthyapus selachops* (fig. 24A). This condition is not uniform throughout the Sphagebranchini, and may vary between and within populations, as evidenced by isolated populations of *Ichthyapus vulturis* (Randall and McCosker, 1975). The Myrophinae lack tp^2 and pop^4. The pop^3 is present in *Ahlia, Myrophis, Pseudomyrophis, Muraenichthys*, and *Schismorhynchus*, but is absent in *Neenchelys, Schultzidia*, and *Benthenchelys* (see Nelson, 1966a, figs. 21-25, in which *Schismorhynchus* was called *Leptenchelys labialis*, and Nelson, 1966b, fig. 1a).

The lateral line ossicles also indicate relationship in their degree of ossification, separation at each pore, and the pore position along the canal. Most pores lie below the midline of the LL canal, although some genera are in having the pores located centrally canal. Lateral line ossicles are nearly tures in the Sphagebranchini and Ca less substantial in the Ophichthini, an duced in the Myrophinae (figs. 22-23).

Certain genera of the Ophichthini a ized in having a well-developed fre neuromast system along the sides and head. The elaborate development of th organs has been generally overloc neuromasts are not randomly scatter the head region, but tend to follow di terns. Nelson (1972) identified these papillae in esocids as "pitlines", whic parently homologous to the free sens masts described herein. Following his ogy, the neuromast lines of *Ophisuru* (fig. 24), beginning at the snout tip paired subnasal, antorbital, anterior, a lines, and a single midline crossing Various degrees of development are als in species of *Ophichthus, Echelus, Piso Quassiremus, Cirrhimuraena, Echiophis, phis*, and *Aplatophis*. The neuromasts minute papillae and are often difficult due to skin rugosity and a waxy precip forms on preserved specimens.

Neuromast development is probably the soft bottom habitat occupied by t cies. Schwartz and Hasler (1966) sugg LL pore development of the mudminn *limi* is reduced and free neuromasts oped in response to its habit of dig soft mud substrate. In doing so, they the pores of the LL canal could become with mud and severly impaired. The and widely distributed superficial org ever would remain functional. Roser Rubinoff (1972: 362) inferred a simil tion in a heterenchelyid eel in n "... the absence of lateral-line pores in indicate that it may be a burrower in or in the semiliquid mud-water interf inverse relation between sensory neuro LL canal development is further eviden ophichthids in that (a) a general corr ists between neuromast development a rather than a sand, substrate occupi species involved, (b) free neuromast de is absent in the Sphagebranchini wher pore development is greatest, and (c) the mud-dwelling species of *Echelus* treme pore reduction and moderate development.

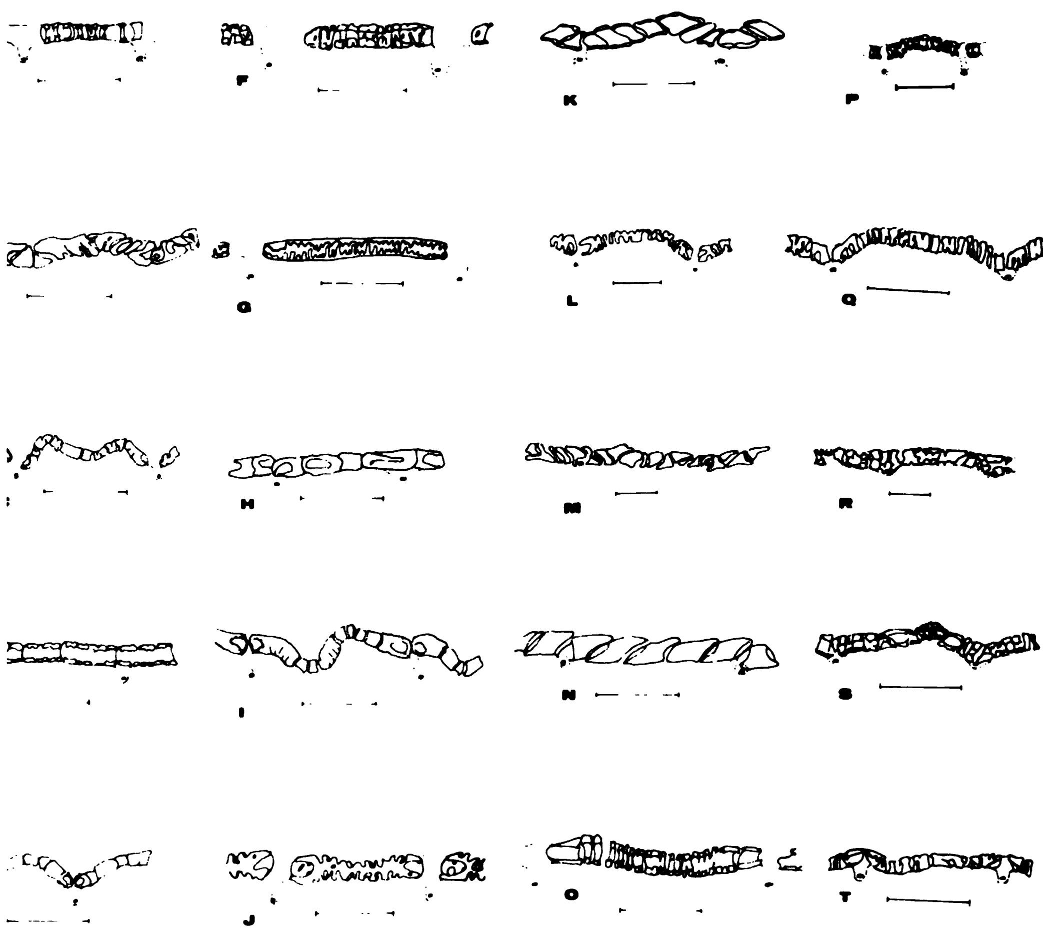


Figure 22. Lateral line ossicles of representative ophichthines. Distal view, right side of mid-trunk region. Scales represent 1 mm. Stippling indicates lateral line canal.

A. *Aplatophis chauliodus*
B. *Quassiremus nothochir*
C. *Phyllophichthus xenodontus*
D. *Aprognathodon platyventris*
E. *Myrichthys xystrurus*
F. *Ophichthus zophochir*
G. *Cirrhimuraena taeniopterus*
H. *Paraletharchus pacificus*
I. *Callechelys eristigmus*
J. *Pisodonophis cancrivorus*
K. *Phaenomonas pinnata*
L. *Ethadophis byrnei*
M. *Ichthyapus selachops*
N. *Yirrkala tenuis*
O. *Caralophia loxochila*
P. *Bascanichthys panamensis*
Q. *Allips concolor*
R. *Cirricaecula johnsoni*
S. *Lamnostoma orientalis*
T. *Elapsopis cyclorhinus*

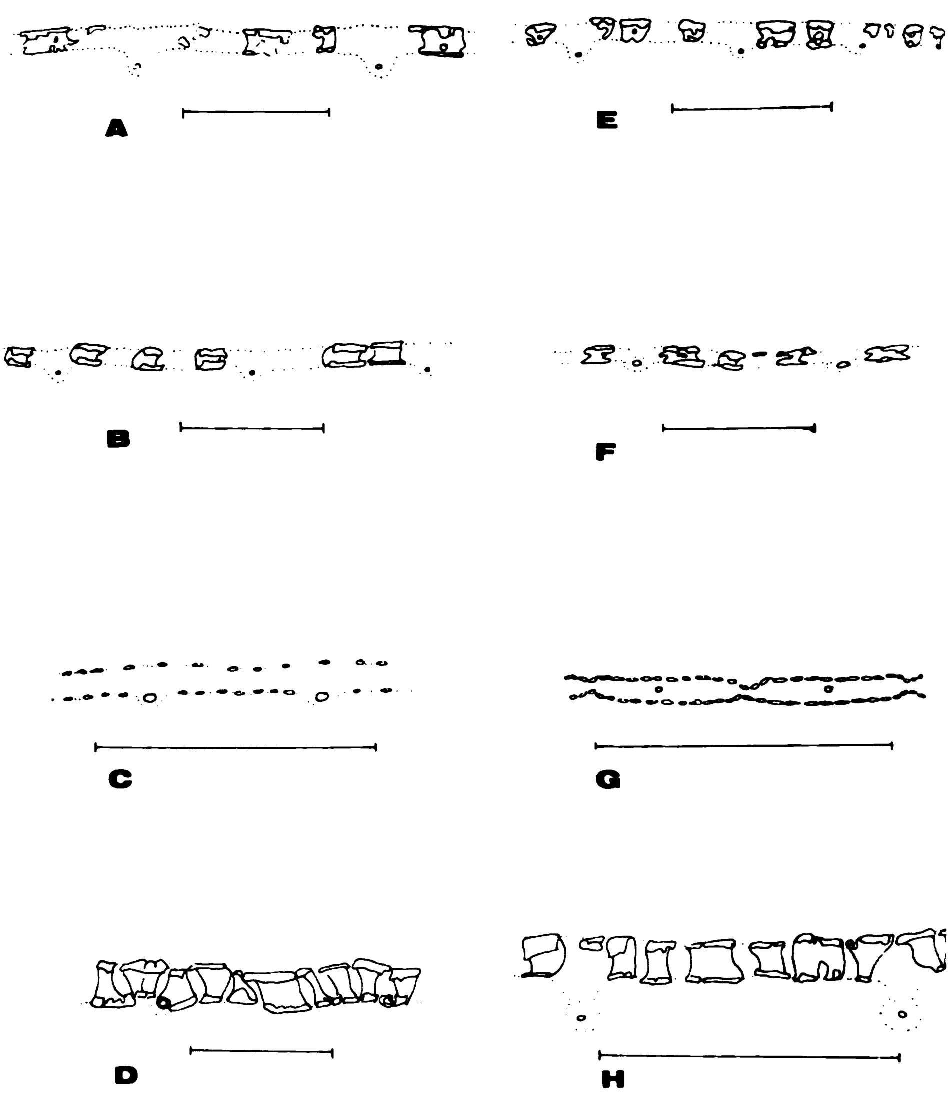


Figure 23. Lateral line ossicles of representative myrophines. Distal view, right side mid-trunk region. Scales indicate 1 mm. Stippling indicates lateral line canal.

A. *Pseudomyrophis nimius*
B. *Myrophis vafer*
C. *Benthenchelys cartieri*
D. *Muraenichthys chilensis*
E. *Pseudomyrophis micropinna*
F. *Ahlia egmontis*
G. *Schismorhynchus labialis*
H. *Schultzidia johnstonensis*

A

B

C

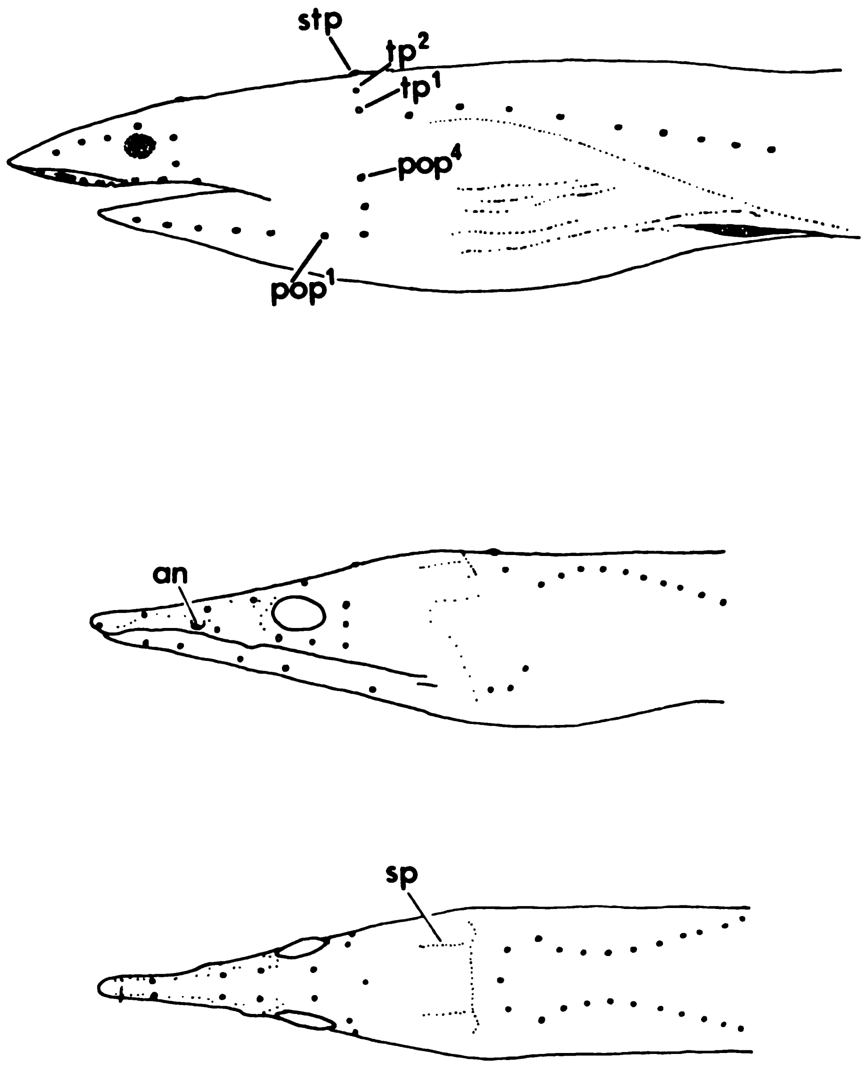


Figure 24. Cephalic pore and surface sensory papillae development in two ophichthids. Abbreviations are: an, anterior nostril; pop', first preopercular pore; sp, surface sensory papillae (free neuromasts); stp, supratemporal pore; tp', first temporal pore.

A. *Ichthyapus selachops*, SIO 65-290. Dotted lines represent contours, not surface sensory papillae.

B. *Ophisurus serpens*, unnumbered Rhodes University specimen, adapted from Allis (1903), left lateral view.

C. *Ophisurus serpens*, dorsal view.

Papillae also occur on the snout and tail tip of several ophichthids (cf. Rosenblatt and McCosker, 1970). Their function has neither been examined nor proposed, but might be inferred from observations and analogous structures on other fishes. Tail tip papillae are generally small and may function as contact sensory devices in relation to the tail-first digging behavior of most observed ophichthids. Certain of the snout papillae are often larger (e.g., in *Leuropharus lasiops* and *Evips percinctus)* and may serve a gustatory as well as a contact sensory function. These papillae are best developed on snouts of several of the small-eyed permanent burrowing species (including species of *Phaenomonas, Bascanichthys,* and *Ichthyapus).* A gustatory function for similar papillae on the snout of a heterenchelid eel might also be inferred from Rosenblatt and Rubinoff's (1972: 362) description of *Pythonichthys asodes.* They observed a reduction in the olfactory epithelium and the development of papillae on the jaws of this small-eyed species, and suggested this was related to a fossorial habit. Most species of ophichthids have not reduced their olfactory epithelium, but probably encounter environmental problems similar to those faced by *Pythonichthys* in their modes of feeding.

Axial Skeleton

Regan (1912) considered the axial skeleton to be of major importance in separating eel families. He separated the Echelidae (considered by Regan to include *Echelus, Ahlia, Myrophis, Paramyrus, Chilorhinus, Muraenichthys,* and *Eomyrus+)* and the Ophichthidae from the Congridae on the basis of the formers' vestigial neural spines. He further separated the Echelidae from the Ophichthidae on the basis of the weaker ribs of the latter family. Gosline (1951a: 302-303) clarified Regan's statements in his discussion of the ophichthid axial skeleton. Difficulties in the preparation and dissection of the anterior vertebrae have precluded their usage in this study in a systematically comparative manner.

The following description is based on the axial skeleton of *Ophichthus zophochir* (figs. 25-26). The first vertebral (V) centrum (CE) is reduced and not fused to the skull (fig. 25A). Its neural arch (NA) extends posteriorly over the second V. A lateral flange on the CE is present on the second and following trunk vertebrae. The NA of V 1-5 are smooth. Along the midline of the NA of V 1-12 is a single longitudinal crest which is split at its posterior margin to fom ridges (fig. 26A). Neural spines (NS) a oped on the trunk vertebrae but beα developed points posterior to the caudal vertebra. Epineurals (EN), epip and pleural ribs (PL) extend posterioι NA and parapophyses (P), and are ap 5-7 V in length. The EN and EP of m thids begin at the posterior margin oi cranium. The P of V 1-12 are posterio and increase gradually in length. mately V 13 the P are symmetrical like normal isosceles triangles. Foram each P, slightly posterior to mid-centru The P of V 13-45 (approximate) are h in size and shape; the lateral proce following 5-6 V are reduced. The first tebra (at which point the haemal arc form) differs markedly in having its upper portion directed laterally to t first caudal transverse process (CTI lower directed downward to become arch (figs. 26C-D). The CTP are sharp jections, incised at their midlines to tl and continuing nearly to the caud haemal arch closure occurs at appro 10th caudal V. The closure howeveι plete, and consists of the joining of tl ends of the haemal spines. Intramι bones replace the neural and pleural caudal region.

Differences in neural arch shape a ing are evident in comparing the five vertebrae of species of the tyr each ophichthid tribe (fig. 25). The of members of the Callechelyini caı guished, at the tribal level, on that Other characters from the axial sk found to be useful indicators of relati parapophyses of certain sphagebran for example, were found to possess process which was lacking in related 33). Also, the CTP are lacking in most yet in *Muraenichthys* and related geı terior half of the column is similar to thine column. Finally, the character pleural ribs of *Ahlia* and *Myrophis* to differ from that of all other ophich they are limited to the anterior 15- (see Remarks concerning *Ahlia* and

Vertebral numbers have been sh useful characters for the separation and populations of apodal fishes. Tl tion to the separation of genera i difficult because of the high degree

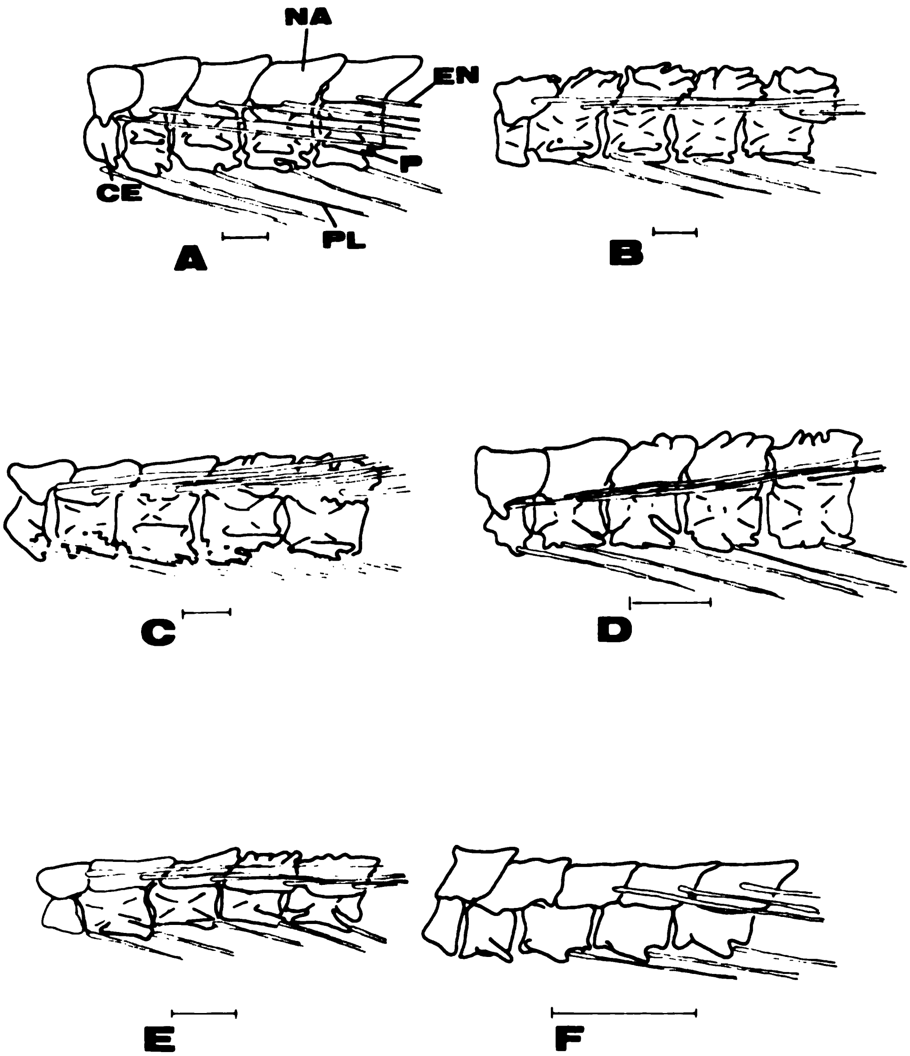


Figure 25. Anteriormost five vertebrae of representative species from the tribes of ophichthids. All are shown in left lateral view. Scale represents 1 mm. Abbreviations are: Ce, centrum; EN, epineural; NA, neural arch; P, parapophysis; PL, pleural rib.

A. *Ophichthus zophochir*
B. *Stictorhinus potamius*
C. *Bascanichthys panamensis*
D. *Callechelys marmoratus*
E. *Myrophis vafer*
F. *Benthenchelys cartieri*

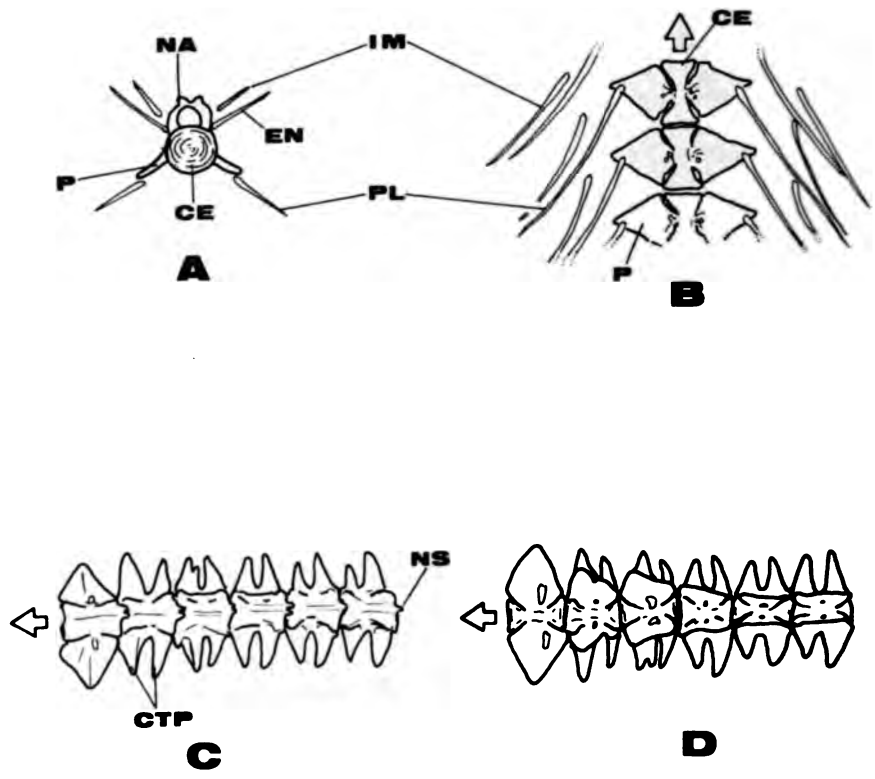


Figure 26. Trunk and caudal vertebrae of *Ophichthus zophochir*. Arrows point anteriorly. Abbreviations are: Ce, centrum; CTP, transverse processes of caudal vertebrae; EN, epineural; IM, intramuscular bone; NA, neural arch; NS, neural spine; P, parapophysis; PL, pleural rib.

A. Anterior view of 14th vertebra. Ribs appear foreshortened due to viewing aspect.
B. Ventral view of 14th-16th vertebrae.
C. Dorsal view of last precaudal (51st) and anterior five caudal vertebrae (52nd-56th). Ribs and IM bones not illustrated.
D. Ventral view of vertebrae illustrated in C. Ribs and IM bones not illustrated.

a, and a single mean value cannot
a genus. Trends, however, are
genera, and are probably relatable
of life and associated anatomical
of the species involved. The spe-
monas, Allips, and *Bascanichthys,*
end to have increased vertebral
arily in the trunk region. An exam-
graphs and gut contents of speci-
genera disclosed the presence of
nd gravel particles in the gut and
the absence of any recognizable
nimal material. On that basis as
ervations of live specimens, I sug-
e eels indiscriminately eat their
he substrate, digesting any utiliz-
naterial they encounter. In many
length of the gut is increased by
ends into the tail portion. The gut
haenomonas and *Bascanichthys* is
nably to prevent blockage by sand
g through the lower tract. The in-
length, which is typical of these
s reflects this problem, and may
cessary to achieve this feeding
callechelyins exhibit a similar in-
vertebrae and a comparable life

mber is also the basis of correlat-
c leptocephalus with the trans-
tage of each eel species. Included
the vertebral numbers of eel spe-
and radiographed in the course
well as several literature records
umed to be correct in species
The literature concerning numbers
rae has not been exhaustively
at errors may inadvertently have
d through improper identification.

n

n the myrophine and ophichthine
emed important enough to most
to recognize the lineages as dis-
The Ophichthidae of nineteenth
was indeed a unique and unified
imarily due to the conspicuously
. Important members, most not-
s of *Echelus,* were erroneously ex-
the Ophichthidae because they
eakly developed caudal fin. Gos-
3) noted the similarity in the oph-
myrophine caudal skeletons, but
continuous median fin condition merited subfamilial separation. His findings, to my knowledge, have not been questioned by subsequent authors. He stated that:

> osteologically, the difference between the tails of *Muraenichthys* and *Cirrhimuraena* is less than that between those of *Cirrhimuraena* and *Caecula platyrhyncha.* Rudimentary rays are present around the tails of both *Muraenichthys* and *Cirrhimuraena;* they are embedded in flesh in *Cirrhimuraena* (as also in *Myrichthys).* In *Caecula platyrhyncha,* on the other hand, there are no rudimentary rays either around the tip of the tail or elsewhere. It is obvious from this discussion . . . that a separate family cannot be maintained for *Muraenichthys* on the basis of tail structure.

The findings of this study are in agreement with Gosline's. Difficulties in the dissection and preparation of the caudal skeleton has precluded its wide usage in this study. Careful examination of certain species however (including *Echelus myrus, E. pachyrhynchus, Leptenchelys vermiformis,* and *Bascanichthys tenuis),* has clarified their position within the family.

The homologies of ossified elements within the apodal caudal skeleton are difficult to determine, and especially so in the case of the sharp-tailed ophichthins and sphagebranchins that have undergone major modification as an adaptation to rapid burrowing. The caudal tip of *Ophichthus zophochir* (fig. 27) is pointed, hard, and without visible caudal rays. The median fins submerge shortly (approximately one eye diameter) before the caudal tip. The underlying osteology is complex, as is illustrated in Figure 27. According to the terminology of Rosenblatt (1967), which was adapted from Nybelin (1963), there is but one weak centrum (CE). Fused to the CE is a pointed hypural (HY) and a much reduced neural arch (NA). Reduced caudal rays (CR) which lack basal elements are imbedded in the skin and weakly associated with the HY. The caudal skeleton of *Myrophis vafer* (fig. 28) differs somewhat from that of *O. zophochir* in possessing a short CE, two elongate HY, and a short cartilaginous extension posterior to each HY. The caudal rays of *Myrophis* are split anteriorly to receive the hypural plate. This is similar to the condition of caudal rays of xenocongrids (Robins and Robins, 1967), but appears to differ from the relatively unspecialized condition of *Anguilla* (Smith and Castle, 1972: fig. 19a). Blache's illustration (1968: figs. 5, 10) of the caudal skeleton of *Echelus* indicates a caudal ray attachment similar to that of *Myrophis.* Present in most apodal

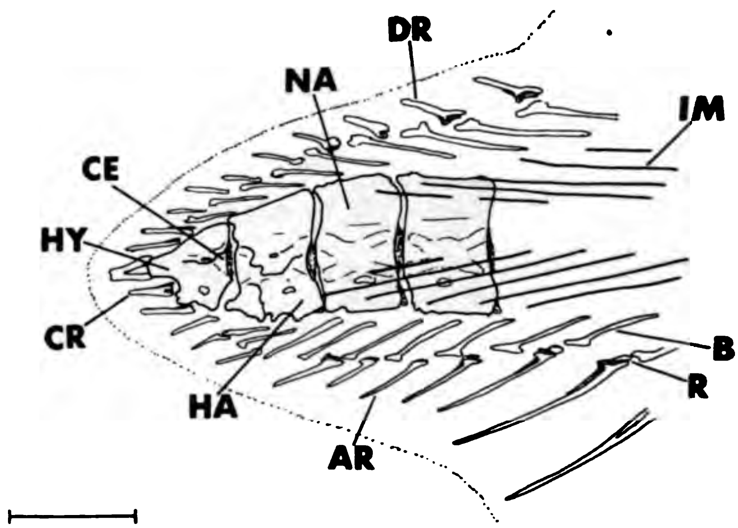


Figure 27. Caudal skeleton of *Ophichthus zophochir*, SIO 65-166. Scale repr
1 mm. Abbreviations are: AR, anal ray; B, basal element of pterygiophore; CE, centrum
caudal ray; DR, dorsal ray; HA, haemal arch; HY, hypural; IM, intramuscular bone
neural arch; R, radial element of pterygiophore.

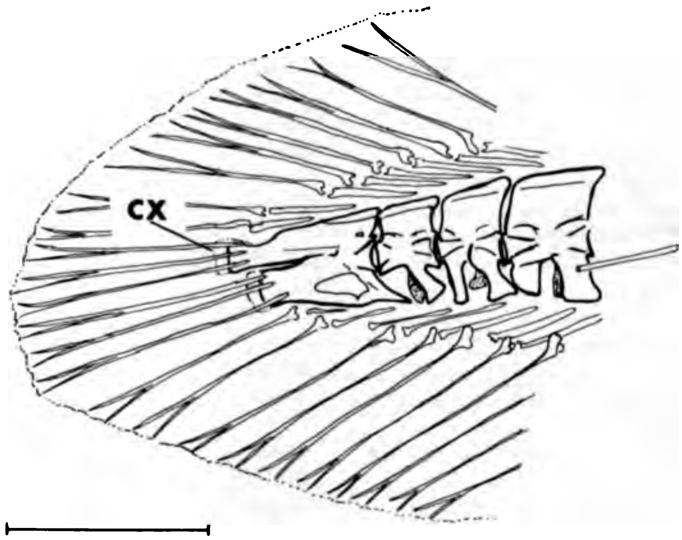


Figure 28. Caudal skeleton of *Myrophis vafer*, SIO 68-242. Scale represents 1 mm. Abbreviation CX is for cartilaginous extension of terminal vertebra.

caudal skeletons is a conspicous foramen beneath the terminal centrum. It is well-developed in *Myrophis*, but reduced or absent in *Ophichthus* and other ophichthines, resulting from the reduction of the lower HY. The haemal aches (HA) of the posterior caudal vertebrae of *Ophichthus* and other ophichthines differs from that of *Myrophis* and other myrophines. The ophichthine condition appears to be that of a simple rectangular lateral plate, whereas in the myrophines a wide gap separates the HA into an anterior and a posterior lateral flange.

The presence of a myrophin-like caudal fin in species of *Echelus* and *Leptenchelys* requires further explanation. As stated above, rudimentary fin rays are present in the sharp-tailed ophichthines. In the discussion of the evolution of the Ophichthidae it is hypothesized that the elongate bascanichthyins separated early in the evolution of the Ophichthinae, and in general, they possess a blunt rather than extremely sharp pointed tail tip. The tail of *Bascanichthys tenuis* is surrounded by a weak epidermis, which without careful inspection gives the appearance of a rayed caudal fin. The caudal tip of *B. tenuis*, when viewed with transmitted light, was found to lack caudal fin rays. The type and only known specimen of *Leptenchelys vermiformis* is similar to *B. tenuis* in possessing loose epidermis at the caudal tip, although minute fin rays appear to be present. The fin ray development in this juvenile specimen may be anomalous, or may represent a redevelopment of the rudimentary fin rays characteristic of the ancestral condition. The caudal fin of *Echelus myrus*, in contrast to the bascanichthyin fins, has well developed fin rays. The caudal skeletons of *Ophichthus zophochir* and *E. myrus* do not markedly differ other than in the development of fin rays. The produced rays appear to be a primitive retention of an ancestral condition, whereas the hard-pointed tail tip of other ophichthines was developed early in the evolution of the family. Other primitive morphological characters of *Echelus* that bear similarities to the generalized ophichthines and certain congrids would suggest that *Echelus* is a primitive ophichthid not far from the basal ophichthine stock.

The caudal skeletons of several ophichthids have been illustrated by earlier authors. Included are: *Benthenchelys cartieri* (Castle, 1972); *Echelus myrus, E. pachyrhynchus*, and *Myrophis plumbeus* (Blache, 1968); *Mystriophis rostellatus, M. crosnieri*, and *Echiophis intertinctus* (Blache,
1971); *Myrichthys pardalis, Basca*
and *Callechelys* spp. (Blache and C
and *Muraenichthys cookei* and
macgregori (Gosline, 1951a).

Visceral Anatomy

The digestive tract and gas blad
shown by Asano (1962) to be us
characters within the Congridae.
concerned primarily with osteolog
anatomy was therefore not exami
tematic manner.

A cursory examination of a myr
phis vafer (SIO 68-286, 240 mm
ophichthine, *Ophichthus zophochi*
335 mm TL), disclosed very sin
tracts and gas bladder morpholo
The digestive tract in both species
diverticulum, or stomach (fide D.
which branches off the anterior tru
extends posteriorly as a blind sac.
in both species examined, is a
opening directly into the anus, wh
ophichthids it appears to extend
the caudal region and then to lo
the anus. The gas bladder (GB) c
iorly to the intestine through the p
(PD) at the mid-trunk level. The
species is thin walled, surround
mesentery, and lies alongside the
dorsally within the peritoneal cavi
white, shiny and flexible; the dig
pale in both species.

The gas bladder of the above-m
cies occupies little of the perito
might be expected from their fo
The GB of the pelagic species *Bent*
tieri however, is considerably lor
of either of the two fossorial s
1972; fig. 25). Its length is appro
third of the trunk length, whereas
are approximately one-fourth to t
GB of congrid eels is longer thar
(cf. Asano, 1962; D. Smith, 1971
the three ophichthids, by contras
ably shorter than the stomach.

TAXONOMY

The following section includes a
definition of the family, a dichoto
the identification of genera, a di
subfamilies and tribes, and an os
external morphological description
of the Ophichthidae.

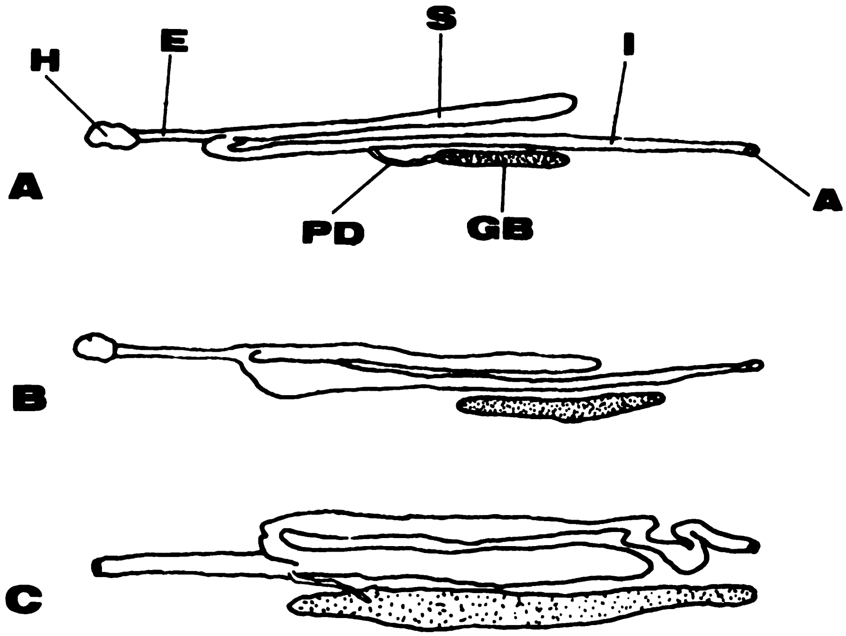


Figure 29. Comparative anatomy of congrid and ophichthid digestive tract and gas ıadder. The gas bladder has been separated from the intestine and the mesentery removed improve clarity. The gas bladder is stippled for identification, not to indicate pigmentation. ɔt drawn to scale. Abbreviations are: A, anus; E, esophagus; GB, gas bladder; H, heart; I, testine; PD, pneumatic duct; S, stomach.

A. *Ophichthus zophochir*, SIO 65-166
B. *Benthenchelys cartieri*, after Castle (1972)
C. *Conger myriaster*, after Asano (1962)

;eneric key is constructed using both ical and external morphological char- n attempt is made to group genera with- ey in a natural manner to indicate rela- ;.

; section, redundancy is avoided wher- ;sible, however in several instances im- :haracters are repeated both in the tribal s and generic descriptions to facilitate ;ons. The generic descriptions are based, r possible, on the type species as well nost morphologically divergent species ach genus, in an attempt to include the variation for each character examined. instances the type species of the genus ıvailable for osteological study. Those re identified in the remarks section fol- ;ach description. The included nominal ɔf each genus are listed under the heading "distribution". Those species known to me only from literature records are indicated by an asterisk (*).

Abbreviations of several morphological characters and conditions are included for the sake of brevity. The reader is referred to the listing of abbreviations in the Materials and Methods of this paper. Also note that Body = Head + Trunk when used in body and tail length comparisons. The symbol $\approx$ means "approximately equal to".

Osteological Definition of the Ophichthidae

From the present study the following osteological definition of the Ophichthidae may be developed:

(a) branchiostegal rays numerous and broadly overlapping along the ventral midline;

(b) supraorbital canals united by a transverse commissure through the fused frontals;

(c) temporal canal present;

(d) frontals of adults fused for their entire length and lacking an obvious suture;

(e) first epibranchial connected by a continuous cartilaginous strap to the second infrapharyngobranchial;

(f) no more than first basibranchial ossified;

(g) third hypobranchial usually cartilaginous;

(h) neural spines rudimentary or absent;

(i) tongue adnate;

(j) palatine absent;

(k) pterygoid well separated from vomer and generally free from hyomandibular.

Analytical Key to the Genera of Ophichthidae

1a. Accessory branchiostegal rays originate behind ends of epihyal (EH), free rays more numerous than attached; caudal fin rays conspicuous, confluent with dorsal and anal, tail tip flexible; gill openings (GO) mid-lateral, a constricted opening .... Myrophinae 2

1b. All branchiostegal rays originate either in association with hyoid or before level of EH tips; free rays, when present, fewer than attached; tail tip a hard or fleshy finless point; GO mid-lateral to entirely ventral, un-constricted ....Ophichthinae........9

2a. Neurocranium short, pointed broad posteriorly, length/depth large, ca. 6 times in head, orbit large, its depth ca. 0.5 skull terior nostril non-tubular; (poste before eye; pectoral fin mod veloped) ....Benthenchelyini .... Ben

2b. Neurocranium more elongate, le $\geqq$ 4; eye smaller, 10 or mor orbital foramen smaller, its d less than 0.5 skull depth; ante tubular .... Myrophini .....

3a. Pleural ribs absent behind 15th vertebra; pectoral fin well devel

3b. Pleural ribs present on all trunk pectoral fin either absent or developed ....

4a. Vomerine teeth absent; dorsal (DFO) above or behind anus; m not tapering posteriorly, and abu goid (fig. 30A); hypohyals (H glossohyal (GH) rudimentary ..

4b. Vomerine teeth present; DFO mid-trunk region; maxilla thin a posteriorly, not closely assoc pterygoid (fig. 30B); HH sepa

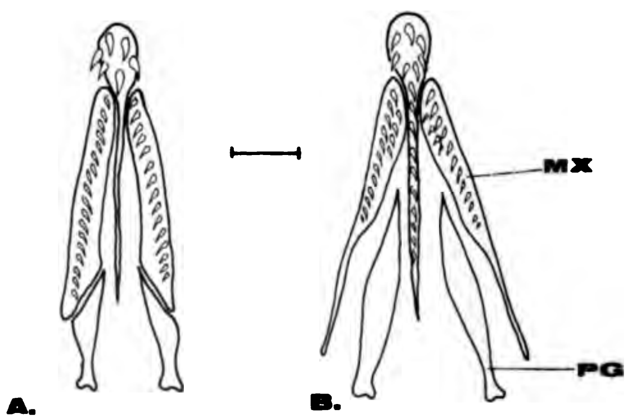


Figure 30. Vomer, maxillae, and pterygoid of *Ahlia egmontis* (A) and *Myrophis* (B). Scale represents 1 mm. Abbreviations are: MX, maxillae; PG, pterygoid.

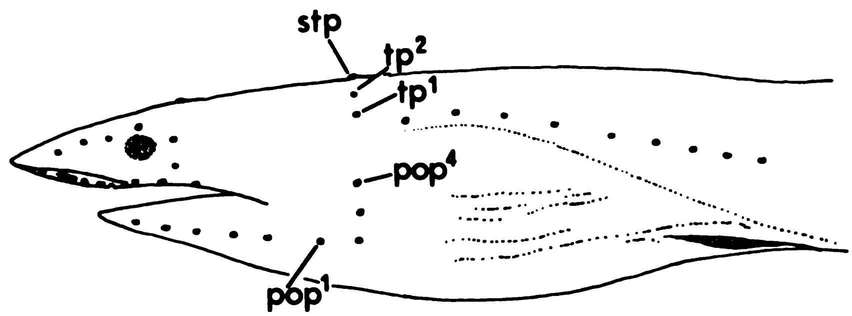


Figure 31. Diagrammatic representation of a species with well developed head pores.

ceratohyal by a gap, GH normally developed .... *Myrophis*

Pectoral fin present, coracoid (Co) and sometimes scapula (Sc) present; posterior nostril lateral; transverse processes of caudal vertebrae (CTP) absent 6

Pectoral fin absent, girdle reduced to cleithrum (Cl) and supracleithrum (SCl); posterior nostril labial; CTP present 7

Pectoral fin minute, Sc and actinosts absent .... *Pseudomyrophis*

Pectoral fin well-developed, Sc, Co, and actinosts present .... *Neenchelys*

Teeth absent on vomer, absent or embedded on intermaxillary, those on maxilla and dentary minute or villiform; supraoccipital (SO) extends anteriorly to frontals, completely separating parietals; SO crest absent .... *Schultzidia*

. Teeth present on intermaxillary, maxilla, dentary, and vomer; SO not extending beyond parietals; SO crest present 8

A prominent toothed groove on underside of snout, bordered by dermal folds, extending anteriorly to anterior nostrils; hypohyals (HH) fused to ceratohyals (CH); suspensorium forwardly inclined .... *Schismorhynchus*

. Underside of snout without a prominent median toothed groove bordered by dermal folds; HH broadly separated from CH by a suture; suspensorium nearly vertical .... *Muraenichthys*

9a. Neurocranium short, terete, length/depth ca. 3 or less; dorsal fin origin (DFO) on nape, above supraoccipital (SO); head pores reduced pop^3, pop^4, and tp^2 absent (fig. 31); hyoid stout, thickened; (gill openings (GO) inferior, parallel or converging forward, isthmus narrower than GO length; pectoral fin absent) ......Callechelyini 10

9b. Neurocranium longer, length/depth 4 or more; DFO, if present, behind nape; head pores generally not reduced, may include pop^3, pop^4, tp^2; hyoid more slender 14

10a. Intermaxillary teeth absent; hypohyals (HH) absent; third hypobranchial (H_3) ossified .. .. *Aprognathodon*

10b. Intermaxillary teeth present; HH broadly separated from ceratohyal by a suture; H_3 cartilaginous 11

11a. Anterior nostril rim not raised; dorsal fin origin (DFO) above epiotics; neurocranium slightly depressed, not convex across parietal-frontal region; four supraorbital pores; (anal fin absent; snout not grooved) .... *Letharchus*

11b. Anterior nostril tubular; DFO above supraoccipital; neurocranium rounded across parietals and frontals; three supraorbital pores 12

12a. Anal fin absent; gill openings (GO) expanded ventrolaterally, forming broad pockets ....*Paraletharchus*

12b. Anal fin present; GO only slightly expanded, not forming broad pockets 13

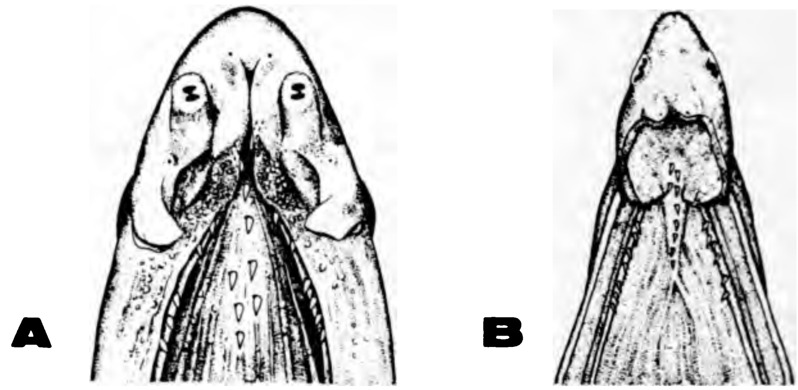


Figure 32. Representation of underside of callechelyin snouts. A. Median groove pre sent (13a in key), as in *Callechelys*. B. Median groove absent, as in *Letharchus*.

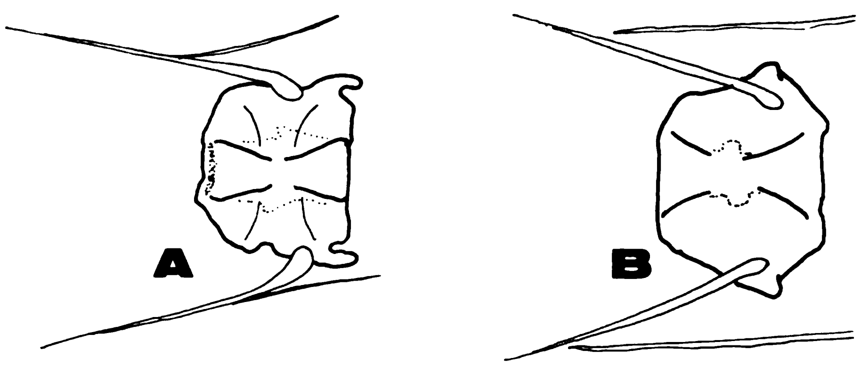


Figure 33. Diagrammatic representation of posterior trunk vertebrae (37th), ventral view. A. Parapophyses with anterior projection (16a in key), as in *Apterichtus*. B. Anterior projection absent (16b in key), as in *Stictorhinus*.

er toothed; median groove on under-
of snout (fig. 32A); snout and nape
heavily papillate ....*Callechelys*
erine shaft toothless; no median
ve on underside of snout; snout and
with numerous papillae ..*Leuropharus*
oral fin absent or vestigial; pectoral
e reduced, consisting of a cleithrum
and may include a supracleithrum
and reduced scapula (Sc) and cora-
(Co); median fins reduced or absent
.... 15
oral fin present, generally well devel-
; pectoral girdle consists of Cl, SCl
pt in *Scytalichthys)*, and generally Sc,
and actinosts; median fins generally
ted .... Ophichthini 29
ocranium depressed and elongate,
n/depth $\geqq$ 4; head pores developed,
nd pop[3] generally present; gill open-
(GO) entirely ventral (except in *Yir-*
..............Sphagebranchini 16
ocranium deeper and shorter, length/
$\leqq$ 4; head pores reduced, tp[2] and
absent; GO low lateral, crescentic ....
nichthyini 22
ns absent; parapophyses of posterior
vertebrae with an anterior marginal
ction (fig. 33a); pectoral girdle re-
l to a cleithrum and a reduced or ab-
supracleithrum; branchiostegal rays
generally fewer than 20 pairs; second
anchial (B_2) absent 17
n fins present; anterior margin of
ior trunk vertebral parapophyses en-
fig. 33b); pectoral girdle includes
um, supracleithrum, and reduced
la and coracoid; branchiostegal rays
numerous, more than 20 pairs; B_2
ginous 19
pharyngeal tooth plates (UP_3 and
used; cirri present on upper lip ....
.... *Cirricaecula*
nd UP_4 separate; upper lip smooth....
.... 18
ior nostril opening outside mouth,
a flap; anterior nostril tubular; eye
ately developed ....*Apterichtus*
ior nostril opening inside mouth,
r without a flap; anterior nostril flush
nout; eye minute ....*Ichthyapus*
head profile, from above, narrows
y from epiotics to interorbital, then
ls evenly to a pointed snout; body
stout, its depth less than 30 in its length; vomerine teeth enlarged, pointed and recurved .... *Lamnostoma*

19b. Lateral head profile narrows evenly from epiotics to snout; body moderately elongate, its depth more than 40 in its length; vomerine teeth conical, not enlarged 20

20a. Eye minute, $\geqq$ 5 in snout; anterior nostril flush along snout; interopercle (IOP) absent .... *Stictorhinus*

20b. Eye larger, $\leqq$ 3 in snout; anterior nostril tubular, or with a short but noticeable rim; IOP present 21

21a. Neurocranium nearly flat across parietals and epiotics; gill openings (GO) with an anterolateral duplication forming a pouch; accessory branchiostegals loosely attached to hyoid, fewer than half associated with epihyal (EH); interopercle (IOP) subrectangular, margin entire ....*Caecula*

21b. Neurocranium raised along dorsal midline, not broad and flat across parietals and epiotics; gill membrane without a duplication; accessory branchiostegals closely associated with hyoid, more than half associated with EH; IOP rounder, serrated along margin ....*Yirrkala*

22a. Tail short, .300-.360 of total length (TL); body extremely elongate, its depth ca. 75-160 times in TL 23

22b. Tail longer, .395-.530 of TL; body not extremely elongate, its depth usually less than 70 in TL 24

23a. Dorsal fin originating just behind occiput and ending less than 2 head lengths behind gill openings; anal fin lacking .... *Phaenomonas*

23b. Vertical fins low, but extending nearly to tail tip ....*Gordiichthys*

24a. Pectoral fin absent; supraoccipital crest (SOC) extends from a parietal ridge, becoming a raised point posteriorly 25

24b. Pectoral fin a minute flap in upper gill opening corner; SOC nearly rounded, little or no posterior point 28

25a. Dorsal fin origin (DFO) behind gill openings (GO); tail longer than body; gill arches stout, third hypobranchial (H_3) ossified, fifth ceratobranchial (C_5) a slender ossified rod ....*Dalophis*

25b. DFO above or behind GO; body $\geqq$ tail; gill arches reduced, H_3 cartilaginous, C_5 absent 26

26a. Anterior nostril not tubular, its rim not raised, developed as an opening with lateral projections into it; underside of snout not grooved; intermaxillary teeth inconspicuous .... *Caralophia*

26b. Anterior nostril tubular; underside of snout grooved; intermaxillary teeth conspicuous 27

27a. Median fins continuous around caudal, caudal fin rays evident .... *Leptenchelys*

27b. Caudal tip blunt, finless .... *Ethadophis*

28a. Dorsal fin origin on head .... *Bascanichthys*

28b. Dorsal fin origin more than a head length behind head .... *Allips*

29a. Fifth ceratobranchial (C_5) absent 30

29b. C_5 present as a slender rod, either ossified or cartilaginous 34

30a. Third preopercular pore (pop^3) present; pectoral fin rudimentary, smaller than eye; pectoral girdle reduced to cleithrum and supracleithrum .... *Quassiremus*

30b. pop^3 absent; pectoral fin well developed, longer than eye; scapula and coracoid of pectoral girdle present 31

31a. Hypohyals (HH) absent; maxilla with a forward projection, articulated ca. mid-vomer; supraoccipital (SO) rounded, lacking a posterior projection; urohyal (UH) deeply notched anteriorly; anterior nostrils with conspicuous leaflike appendages .... *Phyllophichthus*

31b. HH present, separated from ceratohyal by a suture; maxilla without anterior projections, articulated before mid-vomer; SO with a posterior projection; UH not notched beyond midpoint of basal plate; anterior nostrils without leaflike appendages 32

32a. Jaws subequal; upper pharyngeal tooth plates (UP_3-UP_4) separate .... *Pogonophis*

32b. Lower jaw inferior; UP_3-UP_4 fused 33

33a. Third hypobranchial (H_3) ossified; actinosts present; vomerine teeth present .. *Elapsopis*

33b. H_3 cartilaginous; actinosts absent; vomerines absent, or 1-3 small teeth .... *Leiuranus*

34a. Teeth molariform or granular; pectoral fin broad-based (fig. 34A) 35

34b. Teeth pointed; pectoral fin base restricted, opposite upper half of gill openings (fig. 34B) 36

35a. Dorsal fin origin above or behind gill openings (GO); third preopercular pore (pop^3) usually present; hypohyals (HH) narrowly separated from ceratohyal (CH); supraoccipital (SO) with a posterior p
....

35b. DFO well in advance of GO; HH broadly separated fr rounded, without a posterio
....

36a. Eye before middle of upper j portion of neurocranium not yond posterior 2/3, rostral p moid shorter than orbit; son and fanglike ....

36b. Eye over middle of upper ja portion of neurocranium exte or beyond middle of skull; r of ethmoid about equal in le teeth not fanglike ....

37a. Lower jaw projects considera teeth of both jaws long fanglik tending far outside mouth; fr conspicuous sharp ridge ....

37b. Lower jaw inferior or jaws nea anterior teeth in jaws not fan beyond snout tip; frontals n sharp ridge, neurocranium rou dorsally ....

38a. Tail longer than body, compre orly; pectoral developed, 5 or length; third preopercular pore ent ....

38b. Tail shorter than or nearly eq pectoral reduced, 7 or mc length; pop^3 absent ....

39a. Snout short, 7-12 in head len ary cephalic papillae absent ..

39b. Snout longer, 6 or less in l secondary cephalic papillae w
....

40a. Postorbitals strongly develope postorbital strut; branchiostega 20; postorbital region with a transverse depression; lips fri tion uniform .... *Bra*

40b. Postorbitals moderately dev forming a strut; branchiost more; dorsolateral profile of lips entire; body spotted .....

41a. Pectoral fin minute, more tha length; body much longer tha
....

41b. Pectoral fin better developed, length; body and tail nearly s
....

42a. Pectoral fin rudimentary, ≅ longer than tail; (third preop

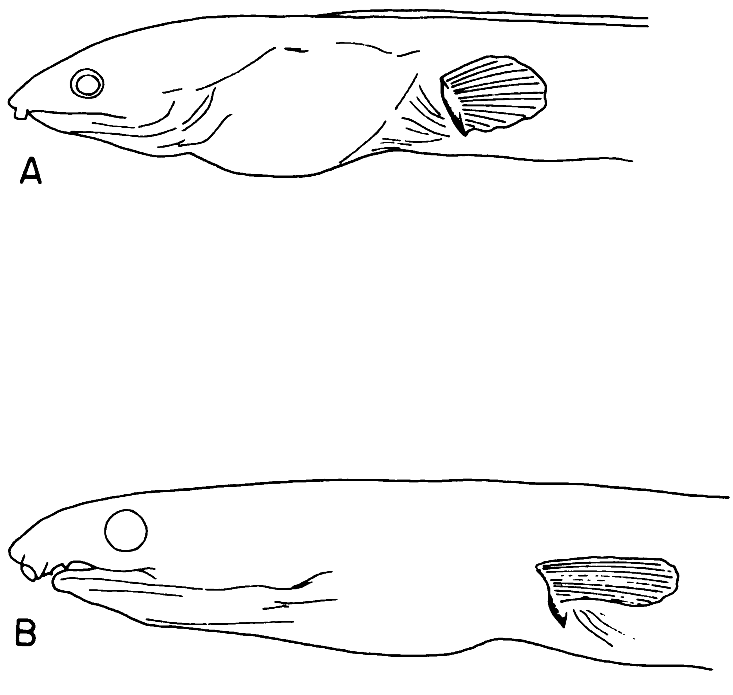


Figure 34. Diagrammatic representation of head and pectoral fin of two ophichthins. A. Pectorals broad-based (34a in key), as in *Myrichthys*. B. Pectoral base restricted (34b in key), as in *Ophichthus*.

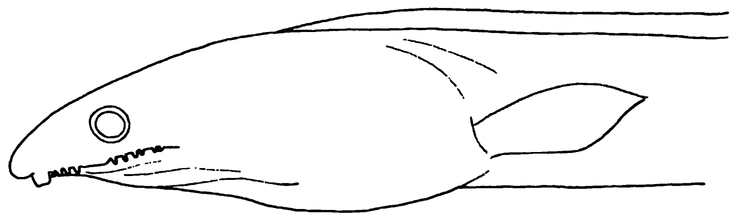


Figure 35. Diagrammatic representation of an ophichthin with a fringed upper lip in key).

absent) ....Evips

42b. Pectoral fin developed, noticeably longer than eye; tail longer than body 43

43a. Caudal fin present, confluent with dorsal and anal; temporal, postorbital, and interorbital pores absent ....*Echelus*

43b. Tip of tail a finless point; temporal, postorbital, and interorbital pores present 44

44a. Dorsal fin origin (DFO) before gill openings (GO); third preopercular pore (pop^3) absent; upper pharyngeal tooth plates (UP_3-UP_4) fused; pectoral girdle reduced, scapula (Sc), coracoid (Co), and actinosts absent ....*Malvoliophis*

44b. DFO behind GO, or if before, the upper lip is fringed; pop^3 usually present; UP_3-UP_4 separate; Sc, Co, and actinosts present 45

45a. Snout very long, attenuate, ethmoid/neurocranium $\geqq$ .500; jaws slender and elongate, incapable of closing completely in adults .. .. *Ophisurus*

45b. Snout moderate or short, ethmoid/neurocranium $<$ .500 jaws not slender and elongate, capable of closing completely..46

46a. Upper lip not fringed, although a barbel may be present; dorsal fin origin (DFO) behind gill openings (GO); opercular series stout, not weak and serrated along margin; actinosts usually 3-4 ....*Ophichthus*

46b. Upper lip fringed (fig. 35); DFO generally on head, or above GO; opercular series weak, subopercle reduced; actinosts 1-2.... .... *Cirrhimuraena*

Kaup's Genera

Kaup published his generic and sp scriptions twice in 1856. The earlier "Ubersicht der Aale" (1856a), is men John Edward Gray in the preface of th the *Catalogue of Apodal fish in the Co the British Museum* (1856b), publish December 1856. Gray stated that "I printing of the work and the engravi plates . . . a synopsis of the genera species has been published by Dr. Kau man, in the *Archiv. fur Naturgeschicht* 1856." Kaup altered several generic the latter work (*Echiophis* became *Ophisurapus* - *Ophisuraphis*, and *Piso Pisoodonophis*), which has resulted spellings of these generic names. Blee emended the spelling of several of K era, but Jordan (1919b) returned to Ka work. In the following listings of gene mies, the pagination of Kaup's later wo will follow that of the earlier, set off theses.

Type species were not designated b his numerous and short-lived gener (1865), as first reviser, synonymized Kaup's genera before types were Jordan seems to have been the first to types for Kaup's invalid genera, and that in each case the first species liste was regarded as the type species (1922).

Subfamilial and Tribal Diagnoses and Generic Descriptions

Subfamily Myrophinae

GO mid-lateral, a constricted open-
ɿind mid-trunk; caudal fin rays not
ırnally visible, confluent with dor-
tail tip flexible; nasals cartilaginous
eratohyal not divided into a short
ı long distal portion (fig. 17B); only
f urohyal ossified, posterior exten-
ɿous; accessory branchiostegal rays
ind tips of epihyal, free rays more
ın attached; branchial skeleton re-
ranchials generally limited to first,
anchial absent; coloration uniform
Jorsally.

Tribe Benthenchelyini

Benthenchelys Fowler, 1934

Body moderately elongate, laterally
ɔehind head; tail much longer than
ɪr nostril not tubular, posterior nos-
ɪfore center of orbit; GO lateral, a
ipse; median fins elevated; pectoral
y developed; head pores enlarged,
ɔpercular pore, frontal commissure
ɔped; LL ossicles fragmentary, near-
ʼurocranium short, rounded (fig. 4);
ɪals, and SOC absent; maxilla broad,
d posteriorly (fig. 16), articulating
ɪrior margin of orbit; gill arches
ed, B_1 cartilaginous, H_3 ossified,
d; pectoral girdle moderately de-
Cl, Sc, and Co present; IM bones
akly developed, CTP absent; epi-
ed to anterior 14-16 vertebrae; ver-
:tive (fig. 25), neural arches promi-
more numerous than precaudal ver-
ation uniform, slightly darker dor-
:haracters those of the single genus.

enthenchelys cartieri was described
934) and referred to the Derichthy-
ebe, 1935). Gosline (1952) referred
ıgridae. Subsequently, Castle (1972)
ɪd it as an ophichthid after a thor-
gical study. The distinctness of this
enus is herein felt to merit tribal
The Benthenchelyini appear to be a
fshoot from the generalized Myro-
ized for a pelagic mode of life. Spe-
nclude the large eye, compressed
ɪd median fins, enlarged head pores,
dentition. These characteristics con-
ıose of other pelagic eels, especially
the genus *Derichthys*. A myrophin relationship, particularly to the generalized *Myrophis*, is evidenced in the hyoid and branchial arches, gill opening, frontal commissure, and disappearance of the epipleural ribs. The pelagic life style of *Benthenchelys* (and the associated eye enlargement), unique to the Ophichthidae, could have evolved from the epipelagic breeding migrations of certain myrophines (see Cohen and Dean, 1970).

Benthenchelys Fowler

Benthenchelys Fowler 1934: 267. (Type species; *B. cartieri* Fowler 1934, by original designation.)

DESCRIPTION (supplementing tribal diagnosis): snout blunt; jaws nearly subequal; eye large; anterior nostril not tubular, a large anteriad opening; DFO slightly before vent; jaw and vomerine teeth conical, recurved, and uniserial, intermaxillary teeth flattened and directed anteriorly, separated from those of vomer by a gap; nasal cartilage weakly developed; suspensorium anteriorly inclined, jaw angle ca. 95°; maxilla broad, not produced posteriorly, articulating beneath anterior margin of orbit; hyoid weak, GH elongate, HH separated from CH by a gap, UH a subrectangular plate anteriorly, a cartilaginous filament posteriorly; branchiostegal rays numerous, 8 along EH, the last 2 joined basally.

ETYMOLOGY: From the Greek βένθος (benthos), deep, and ἔγχελυς (enchelys; either masculine or feminine, here to be treated as masculine), eel.

DISTRIBUTION: A single pelagic species (100-250 meters) over deep water in the central Indo-Pacific.

Tribe Myrophini

TYPE GENUS: *Myrophis* Lütken, 1851

DIAGNOSIS: Body short to extremely elongate, laterally compressed behind head; tail generally longer than body; lower jaw included; anterior nostril tubular; posterior nostril either lateral or labial; GO lateral, a constricted opening; median fins low or elevated, DFO behind mid-trunk; pectoral fin present or absent; head pores variably developed; LL canal weakly ossified; intermaxillary dentition and vomerine, when present, continuous; neurocranium not raised along frontal or parietal midline, SO crest developed in

some genera; orbit moderately developed; gill arches reduced, weakly ossified, B_1 often absent, B_{2-4} absent or rudimentary; pectoral girdle development variable; IM bones and ribs moderately to weakly developed, transverse processes of caudal vertebrae present in some genera; epipleurals limited to anterior trunk vertebrae in some genera; caudal vertebrae more numerous than precaudal; coloration uniform, often darker dorsally.

Ahlia Jordan and Davis

Ahlia Jordan and Davis 1891: 639. (Type species; *Myrophis egmontis* Jordan 1889, by original designation.)

DESCRIPTION: General characters those of *Myrophis*. Differences include: snout sub-conical, broad; DFO above or behind anus; vomerine teeth absent; maxilla broad, not tapering posteriorly, closely abuts the short and broad pterygoid (fig. 30); HH absent, GH rudimentary; gill arches reduced, H_3 and I_2 absent.

ETYMOLOGY: Named for Jonas Nicolas Ahl, author of "De Muraena et Ophichtho", with the noun suffix *-ia* (neuter).

DISTRIBUTION: A single Caribbean species.

REMARKS: The controversy regarding generic synonymy of *Ahlia* has never involved a detailed osteological study. Those considering it synonymous with *Myrophis* (Parr, 1930: 8; Hildebrand, in Longley and Hildebrand, 1941: 17; Schultz and Woods, 1949: 171) did not consider the absence of vomerine teeth to represent a generic character, but it was assumed by Jordan and Davis (1891: 639), Myers and Storey (1939: 158), and Wade (1946: 199) that this warranted separation. Nelson (1966a: 398) considered *Ahlia* to be distinct on the basis of gill arch characters. The generic differences that I have identified are clearly related to feeding specialization in *A. egmontis*, viz., tooth loss, maxillary-pterygoid bracing, and gill arch reduction, yet the universality of these characters among the species of *Myrophis* suggests that the species of *Myrophis* form a natural group from which *Ahlia* is a specialized offshoot.

Cohen and Dean (1970) have recorded an interesting observation of offshore movements and a change in eye size accompanying the onset of sexual maturity in this species. Their observations were made off Honduras, approximately 145 km from shore. I have made similar observations within I km from land in the
Archipelago, off the Atlantic coast of P

Muraenichthys Bleeker

Muraenichthys Bleeker 1853b: 505. (T
cies; *M. gymnopterus* Bleeker 1853, b
designation.)

Scolecenchelys Ogilby 1897: 246. Spel
chelys by other authors. (Type speci
aenichthys australis Macleay 1881, by
designation.)

Myropterura Ogilby 1897: 247. (Type
Myropterura laticaudata Ogilby 1897,
nal designation.)

?*Aotea* Phillipps 1926: 533. (Type specie
acus Phillipps 1926, by monotypy.)

DESCRIPTION: Body short to moderatel
ate, tail generally longer than body, later
pressed posteriorly; snout sub-conical t
not deeply grooved on underside; poste
tril either along edge of lip beneath a
opening into mouth; DFO from mid-
well behind anus; pectoral fin absent; p
ent; LL ossicles continuous, well develop
myrophin; dentition variable, teeth ofte
serial, either conical or blunt, dentition c
continuous with that of intermaxillary; s
truncate posteriorly; SOC present; maxil
ate, slender posteriorly (fig. 16); susp
nearly vertical; opercular series weakly
subopercle generally rudimentary, produ
teriorly in some species (as in *Myrophis*,
otic bulla weakly developed; PG short,
ing maxillae, reduced and slender in
genus; HH separated from CH by a nar
gill arches reduced, basibranchials abse
sified and UP_3-UP_4 fusion variable;
girdle reduced to a slender CI and SCI;
ribs on all precaudal vertebrae; CTP m
developed.

ETYMOLOGY: From the Greek μύ
an eel, and ἰχθύς (ichthys; mascul

DISTRIBUTION: Nineteen recognized
from the tropical, subtropical, and warm
ate Indo-Pacific Ocean, including a singl
from the eastern south Pacific. Material
undescribed Red Sea and western Pacifi

REMARKS: Subgeneric lines within *Mura*
were indicated by McCosker (1970)
not designated pending a thorough os
study. My examination and comparis

M. chilensis, and *M. macropterus* 'er osteological differences compar- used to separate other closely re- hid genera. This result was unex- ıt the external morphology differs within the genus, including differ- ut form (from blunt to acute), in 15-50 times in total length), in the ıosition of head pores, in dentition, ıracter of the posterior nostril. Sub- may be identified in the following

ıstril opens on the outer lip as an t with an anterior flap; a single ›en the anterior and posterior v teeth usually in bands, inter- eth in a patch; UP_3-UP_4 fused in nined; snout usually blunt; body t, its depth ca. 15-25 in TL .... Subgenus *Muraenichthys* Bleeker

ıstril opens into mouth, covered ·ior valvular flap; two pores be- rils; jaw teeth uniserial or bi- maxillary teeth not in a broad -UP_4 separate in species exam- usually acute; body moderately ; depth usually more than 25 in Subgenus *Scolecenchelys* Ogilby

Muraenichthys includes *M. gym-* ·ker (the type species), *M. hattae* ›nyder, *M. schultzei* Bleeker, and ıacrostomus Bleeker, *M. philippin-* ınd Woods, *M. sibogae* Weber and nd *M. thompsoni* Jordan and Rich- subgenus *Scolecenchelys* includes lacleay* (the type species), *M. chil-* er, *M. acutirostris* Weber and de *ookei* Fowler, *M. gymnotus* Bleeker, *us* Bleeker, *M. breviceps* Günther, *M. iredalei* Whitley. Also included *thys*, but not here allocated to a ː *Myropterura laticaudata* Ogilby, *'ermiformis* Peters, *Muraenichthys* *M. xorae* Smith*, and *M. godeffroyi* ›ecimens of *M. macropterus* dis- lelson's (1966a) description in hav- l UP_3-UP_4.

ı *Muraenichthys*, *Schultzidia*, and ıus display obvious similarities at- a common ancestry. Primitive and ›itions of certain characters may be ong the approximately 24 species involved (many of the species included are known to me only from the literature and not from specimens). For example, postulated primitive conditions include the moderately elongate body, sub-conical snout, posterior nostril opening into the mouth, numerous head pores, uniserial or biserial conical teeth, presence of the SO crest, posterior development of the subopercle, separate hypohyals, ossified second infrapharyngobranchial, separate UP_3-UP_4, and conspicuous cleithrum and supracleithrum. Species of the subgenus *Scolecenchelys* are clearly the most primitive, with the species of the subgenus *Muraenichthys*, and *Schultzidia and Schismorhynchus* as specialized offshoots. The development of transverse processes on the caudal vertebrae, shared by these genera, is unique among the Myrophinae and without apparent antecedents in more primitive genera such as *Myrophis*.

Aotea, type species *A. acus*, was described by Phillipps (1926) on the basis of a partially digested specimen from New Zealand waters, and placed in *Muraenichthys* by Castle (1967). Whitley (1968) placed *A. acus* in the synonymy of *Muraenichthys breviceps* Günther, yet Phillipps (1926: 533-534) characterized *A. acus* as having "fins absent" and "a hard folded portion beneath body posterior to head apparently indicat(ing) gill-openings . . .", both of which would exclude *Aotea* from the subfamily Myrophinae. Phillipps' sketchy description of *A. acus* does not obviously agree with any known ophichthine genus, but best fits *Apterichtus*, *Ichthyapus*, and *Cirricaecula*. Further examination may discover that *Aotea acus* is a species of *Apterichtus* in that the species of the latter two genera are not known from even as far south as Australian waters.

Myrophis Lütken

Myrophis Lütken 1851: 14. (Type species; *M. punctatus* Lütken 1851, by monotypy.)

Paramyrus Günther 1870: 51. (Type species; *Conger cylindroideus* Ranzani 1838, by Jordan and Davis (1891) as first revisers.)

Holopterura Cope 1871: 482. (Type species; *H. plumbea* Cope, 1871, by monotypy.)

Hesperomyrus Myers and Storey 1939: 157. (Type species: *H. fryi* Myers and Storey 1939 = *Myrophis vafer* Jordan and Gilbert, by original designation.)

DESCRIPTION: Body stout to moderately elongate, laterally compressed throughout; snout sub-

conical to conical and moderately elongate; eye moderate; posterior nostril along edge of lip beneath a flap or opening into mouth; DFO before mid-trunk region; pectoral fin moderately developed, longer than eye; pop^3 present; teeth conical, uniserial or biserial in jaws and vomer; skull subtruncate posteriorly (fig. 5); SOC present; maxilla elongate, slender posteriorly (fig. 30B); subopercle produced posteriorly as a posteroventral border to the opercle (fig. 36); otic bulla weakly developed; PG short, not bracing maxilla; H_3 cartilaginous, UP_3-UP_4 fused in one species; Cl and SCl slender, Sc, Co, and an actinost (?) well developed; epipleural ribs limited to anteriormost 15-20 vertebrae; CTP absent.

ETYMOLOGY: From the Greek μύρος, Myrus, and ὄφις (ophis; masculine), snake.

DISTRIBUTION: A circumtropical genus of nine nominal species. Included are: *Myrophis punctatus* Lütken (WA), *M. australis* Castelnau (IP)*, *M. cheni* Weng (IP)*, *M. lepturus* Kotthaus (IP)*, *M. platyrhynchus* Breder (WA)*, *M. vafer* Jordan and Gilbert (EP), *Conger uropterus* Temminck and Schlegel (IP), *C. cylindroideus* Ranzani (EA)*, *Holopterura plumbea* Cope (EA). *Incertae sedis: Myrophis frio* Jordan and Davis (WA)*.

REMARKS: Schultz, et al. (1953: 68) erroneously included *Parabathymyrus* Kamohara in the synonymy of *Myrophis*. D. Smith (1971) recognized it as a valid congrid genus of the subfamily Bathymyrinae.

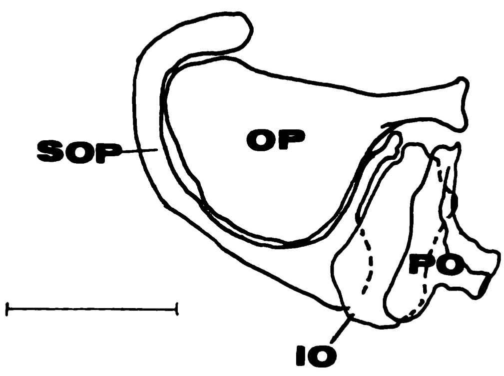


Figure 36. Opercular series of *Myrophis vafer*, SIO 68-242. Right side, distal view. Scale represents 1 mm. Abbreviations are: IO, interopercle; OP, opercle; PO, preopercle; SOP, subopercle.

Castle (1963: 16) has discussed
the congrid *Gnathophis heterogn*
which has been erroneously incl
phis by recent authors.

Neenchelys Bamber

Neenchelys Bamber 1915: 479.
N. microtretus Bamber 1915, by

DESCRIPTION: Body moderately
pressed posteriorly; body shorter t
sub-conical; eye moderate; poste
elongate slit before lower margin
before mid-trunk; pectoral fin n
veloped, longer than eye; pop^3
conical, uniserial except at vomer
maxillary; skull rounded posteriorl
tion unknown; SOC absent; maxill
slender posteriorly; subopercle
posteriorly (fide Nelson 1966b, fig
weakly developed; B_1 rudimenta
UP_3-UP_4 separate; pectoral girdle
Cl, Sc, Co, and an actinost (?) pr
ral rib condition unknown.

ETYMOLOGY: Presumably from th
new, and ἔγχελυς (enchel
masculine, treated as masculine b

DISTRIBUTION: Two species,
Bamber* from the Red Sea, and
Weber and de Beaufort* from the

REMARKS: Specimens of *Neench*
available for this study. The des
pared from Nelson's (1966b) o
Mohamed's (1958) morphological
N. buitendijki. Nelson (1967) note
of overlapping branchiostegals i
of *N. microtretus* (apparently th
specimen) but did not compare it
dijki.

Nelson (1966b: 323), in commen
(1946) description of *Pseudom*
pinna, stated that "there is no cl
cant enough to maintain *Pseudo*
genus distinct from *Neenchelys*.
the other hand, seems distinctive
placed in a genus of its own."
examination of the species of *P*
which I have found to be con
further comment on this relation
genera show certain similarities
and habitat (living in mud bottom
deep water) and are more closely
other than to other genera. Oste
larities include the shapes of th

ıaxillae, gill arches, hyoid arches, ertebrae. The characters used in the ɔ separate these genera may be ex- : following manner:

erior trunk region; snout conical; ı well developed, ≅ snout; pop^{3} bopercle small, sub-rectangular; ;ubopercle condition of *N. micro-* ıown) ....*Neenchelys*

;terior trunk region; snout broad, :toral fin minute, ≦ eye; pop^{3} ubopercle produced posteriorly ral and posterior margins of op- ....*Pseudomyrophis*

Pseudomyrophis Wade

his Wade 1946: 199. (Type species; *ına* Wade 1946, by original designa-

ɺ: Body moderately to extremely rally compressed throughout; snout ; eye small to moderate; posterior ɔngate slit before lower margin of ›ehind mid-trunk; pectoral fin min- :han eye; pop^{3} present; teeth coni- throughout, except at anterior vo- ermaxillary; skull rounded posteri- ɔssified along canal only, nasal car- ' developed; SOC absent; maxilla ıder posteriorly; subopercle similar (Fig. 36), produced posteriorly as a eroventral border to opercle; otic developed; PG short, not produced ı and I_2 ossified, UP_3-UP_4 separate; le reduced to Cl and SCI (and frac- ı *P. micropinna);* epipleural ribs on vertebrae.

: From the Greek ψευδής lse, -o-, and *Myrophis* (masculine), ›hichthids.

·N: Two New World species, *P. ni-* : (Caribbean) and *P. micropinna* n Pacific).

he species of *Pseudomyrophis* are 'ferent in body depth and head ın osteological comparison did not erences that are clearly generic. rtional differences are also related ·me elongation of *P. nimius*. The :nce in vertebral number between ;0) is less than that between species of *Phaenomonas* (ca. 70). Both species are apparently adapted to soft mud bottoms in water relatively deep for ophichthids (*P. micropinna* from depths of 45-60 fms, *P. nimius* to 400 fms).

Schismorhynchus McCosker

Schismorhynchus McCosker 1970: 509. (Type species; *Muraenichthys labialis* Seale 1917, by original designation.)

DESCRIPTION: General characteristics those of *Muraenichthys*. Differences include: body moderately elongate; body shorter than tail; snout conical, elongate, with a prominent toothed groove on underside; anterior nostril an elongated tube as long as eye; posterior nostril opens into mouth; DFO in posterior trunk region; pop^{3} and median interorbital pore absent; teeth conical, uniserial; maxilla broad, not becoming slender posteriorly; subopercle produced posteriorly as in *Myrophis* (fig. 36); suspensorium anteriorly inclined; HH fused to CH (or absent?), GH rudimentary; gill arches extremely reduced, B_1, H_3, and I_3 absent, UP_3-UP_4 fused, lower tooth plate elongate (see Nelson, 1966a: figs. 14-15); pectoral girdle reduced to a slender Cl.

ETYMOLOGY: From the Greek σχισμή (schisme), cleft, and ῥύγχος (latinized as rhynchus, masculine in accordance with item 30(a)(3) of the International Code of Zoological Nomenclature), nose.

DISTRIBUTION: A single species, widespread in the central and western Pacific ocean.

Schultzidia Gosline

Schultzidia Gosline 1951a: 309. Described as a subgenus of *Muraenichthys* Bleeker. (Type species; *Muraenichthys johnstonensis* Schultz and Woods 1949, by original designation.)

DESCRIPTION: General characteristics those of *Muraenichthys*. Differences include: body stout to moderately elongate, body shorter than tail; posterior nostril opens into mouth; DFO behind anus; pop^{3} absent; teeth absent on vomer, absent or imbedded on intermaxillary, those on maxilla and dentary minute or villiform; SOC absent, SO extends anteriorly to frontals, completely separating parietals; opercular series rudimentary, subopercle not produced posteriorly; PG slender; hyoid rudimentary, HH separated from CH by a gap, UH fragmentary, separated medially; gill arches extremely reduced, B_1 and I_3

absent, UP_3-UP_4 fused, tooth plates elongate and vermiculated; CTP weakly developed.

ETYMOLOGY: Named for Leonard P. Schultz, ichthyologist, with the assumed noun suffix *-idia* (feminine).

DISTRIBUTION: Two central and western Pacific species, described as *Muraenichthys johnstonensis* Schultz and Woods, and *M. retropinnis* Seale.

Subfamily Ophichthinae

DIAGNOSIS: Gill opening variable, mid-lateral to entirely ventral and longitudinal, generally elongate and unconstricted; DFO variable, from nape to behind anus; tail tip generally a hard finless point, rudimentary rays visible in certain genera; nasals ossified, generally well developed, but reduced or absent in certain genera; CH divided into a short median and longer distal portion, the median section connecting to the CH by a cartilaginous splint (see fig. 17A); UH generally continues posteriorly from basal plate as a slender ossified spike; all branchiostegal rays originate either in association with hyoid or before level of EH tips; gill arch skeleton variably developed, first basibranchial always ossified, second through fourth generally present in either a cartilaginous or rudimentary condition, C_5 present in several genera; coloration variable, banded, barred, striped, spotted, or uniform patterns.

Tribe Callechelyini

TYPE GENUS: *Callechelys* Kaup, 1856

DIAGNOSIS: Body (head and trunk) and tail moderately elongate, laterally compressed; body longer than tail; snout acute, rounded at tip; lower jaw included; eye small; posterior nostril opens into mouth; GO low lateral to entirely ventral, converging forward, length much greater than isthmus width; dorsal fin originating on nape; pectoral fin absent; tail tip a hard finless point; head pores reduced, pop^3 and tp^2 absent; LL ossicles nearly continuous; teeth conical, jaw teeth uniserial, those of vomer separated from those of intermaxillary by a gap; skull short, sloping posteriorly, its height ca. 3 or less in its length (fig. 7); orbit moderately developed; SO rounded, without a posterior projection; PG slender, elongate, free and tapering posteriorly; margin of opercular series irregularly ossified, with cartilaginous gaps; suspensorium nearly vertical; otic bulla well developed; hyoid stout; branchiostegal rays numerous; gill arches reduced, C_5 absent, UP_3-UP_4 sepa girdle reduced to Cl, SCl, and 1 o elements; IM bones, ribs, and C precaudal vertebrae more numerou coloration variable, either striped, ted, mottled, or uniform.

REMARKS: The Callechelyini const distinct and compact of ophichthi able material or radiographs of 19 cies of Callechelyini has allowed study of this tribe. The results of programmed numerical taxonomi of this tribe are presented in the tion. Several important morphologi logical characters of the species Table 8.

Aprognathodon Böhlk

Aprognathodon Böhlke 1966: 99. *A. platyventris* Böhlke 1966, by nation.)

DESCRIPTION: Anterior nostril t moderate, rounded at tip; median on underside of snout; intermaxil sent, vomerine teeth present; DF anal fin present; 3 supraorbital cranium well rounded, highest ant al-parietal suture; hyoid arch ver ible along CH-EH suture; HH abs stegal rays numerous, along arch basally, distal 4-6 rays along EH b ally; UH a simple cartilaginous p teriorly, basal plate ossified; gill a partially or completely ossified; contains Cl, SCl, and 2 rod-sha body coloration strongly banded

ETYMOLOGY: From the Greek πρό (pro), forward, γνάθ jaw, and ὀδών (odon; mascu reference to the lack of intermaxi

DISTRIBUTION: A single western A known from the Bahamas through tilles to Venezuela.

Callechelys Kaup

Callechelys Kaup 1856: 51 (28). *C. guichenoti* Kaup 1856 = *Dal ata* Bleeker 1853, by monotypy.)
Cryptopterygium Ginsburg 1951: cies; *Cryptopterygium holochi* 1951, by original designation.)

: Anterior nostril tubular; snout d at tip; a median groove on un-out (Fig. 32A); intermaxillary and th present; DFO above SO; anal supraorbital pores; neurocranium highest anterior to level of frontal- (fig. 7); hyoid arch stout, moder-along CH-EH suture; HH separated a narrow gap; branchiostegal rays ong arch; distal rays along EH sally in some species; UH either a r filament posteriorly, or split into t rays; H_3 cartilaginous; pectoral s Cl, SCl, and either one or two ements; coloration variable, either ed, mottled, or banded.

Kaup (1856a, b) did not give the the generic name nor did he desig-r. From his description (1856b: 28), ie eel . . .", one must assume that the generic name to be derived λος (beauty) and ἔγχελυς which is feminine, but according Scott (1801), was later also mascu-(1865), as first reviser, further con-by recognizing *Dalophis marmor-* *Callechelys marmoratus* and also *allechelys melanotaenia*. To date, f *Callechelys* has not been estab-gh the most recent revisers (McCos-nblatt, 1972) have regarded *Calle-* culine.

N: A cosmopolitan genus with 15 ubtropical species. Nominal species *echelys bilinearis* Kanazawa (WA), ke and Briggs (EP), *C. eristigmus* d Rosenblatt (EP), *C. galapagensis* d Rosenblatt (EP), *C. luteus* Snyder *notaenia* Bleeker (IP), *C. muraena* rermann (WA), *C. nebulosus* Smith e *Storey* (WA, EA), *C. striatus* Smith *ys bitaeniatus* Peters (IP)*, *Crypto-lochroma* Ginsburg (WA), *Caecula* idenat (EA)*, *Dalophis marmorata* *Gordiichthys springeri* Ginsburg

umerous authors (Günther, 1910: i, 1912; Storey, 1939: 63; Smith, Cosker and Rosenblatt, 1972: 22) d the validity of *C. guichenoti*, the with the majority supporting its th *C. marmoratus*. Marie-Louise Bauchot of the Paris Museum has kindly furnished measurements and a radiograph of the type specimen (MNHN 2126) of *C. guichenoti*. Its morphometry and osteology (183 vertebrae and a single pectoral girdle horizontal element) are further evidence of its synonymy with *C. marmoratus*.

Subgeneric lines within *Callechelys* were suggested by McCosker and Rosenblatt (1972). They recognized two major groups, one containing species with a simple urohyal and a single rod-shaped pectoral element (fig. 19L) and another with species having the urohyal split posteriorly into two slender divergent rays and two rod-shaped pectoral elements (as in *Aprognathodon*, fig. 19M). A third can be recognized, which possesses a mosaic of characters, including slightly broadened branchiostegal rays along the epihyal, and urohyal and pectoral girdle conditions that do not conform to either of the above groups. Programs REGROUP and WVGM showed little affinity between *C. nebulosus* of this last group and the remainder of the genus. It appears that the simple urohyal, broadened rays, and paired girdle elements are primitive conditions within the Callechelyini, characters shared by *C. nebulosus* and *C. springeri*.

Letharchus Goode and Bean

Letharchus Goode and Bean 1882: 437. (Type species *L. velifer* Goode and Bean 1882, by original designation.)

DESCRIPTION: Anterior nostril a hole, its rim not raised; snout moderate, acute, not rounded at tip; median groove on underside of snout absent (fig. 32b); intermaxillary and vomerine teeth present; DFO above epiotics; anal fin absent; four supraorbital pores; neurocranium depressed, not rounded across parietal-frontal region, highest at frontal-parietal suture; hyoid arch stout, flexible along CH-EH suture, HH separated from CH by a gap; branchiostegal rays numerous, slender, all along arch; UH a slender filament posteriorly; H_3 cartilaginous; pectoral girdle contains Cl, SCl, and 2 rod-shaped elements; body coloration uniformly dark, contrasting strongly with the white dorsal fin.

ETYMOLOGY: From the Greek λήθομαι to forget, and ἀρχός (archos; masculine), anus, in reference to the lack of an anal fin.

DISTRIBUTION: Known from three New World species: *L. velifer* from the western Atlantic

(North Carolina to the northern Gulf of Mexico), *L. aliculatus* McCosker from off Brazil, and *L. rosenblatti* McCosker from the eastern Pacific.

REMARKS: The genera *Letharchus* and *Paraletharchus* were recently revised by McCosker (1974). The species of *Letharchus* form a unique and distinctive offshoot from the generalized callechelyin condition in their combination of anal fin absence, non-tubular nostrils, an additional supraorbital pore, and the acute snout, differing markedly from the characters of other genera within the tribe. *Letharchus pacificus* Osborne and Nichols and *L. opercularis* Myers and Wade are obviously similar to the above species in lacking an anal fin, and probably for that reason were assumed by their describers to be congeneric with *L. velifer*. After examining considerable material and the types of these five species I have concluded that *L. opercularis* and *L. pacificus* represent a separate generic line within the Callechelyini.

The osteological description of *Letharchus* is based on the eastern Pacific species in that material of *L. velifer* was unavailable for dissection.

Leuropharus Rosenblatt and McCosker

Leuropharus Rosenblatt and McCosker 1970: 502. (Type species; *L. lasiops* Rosenblatt and McCosker 1970, by original designation.)

DESCRIPTION: Anterior nostril tubular; snout short, rounded at tip; median groove on underside of snout absent; snout, nape, and much of surface of jaws papillate; intermaxillary teeth present, vomerine teeth absent; DFO above SO; anal fin present; three supraorbital pores; neurocranium well rounded, highest anterior to frontal-parietal suture; HH separated from CH by a gap; branchiostegal rays numerous, slender, and along arch; H_3 cartilaginous; pectoral girdle contains Cl, SCl, and 2 rod-shaped elements; body coloration nearly uniform, median fins white.

ETYMOLOGY: From the Greek λευρός (leuros), smooth, and φάρος (pharos; neuter), plow, in reference to the toothless vomer.

DISTRIBUTION: A single species, known only from the type specimen from Manzanillo Bay, western Mexico.

Paraletharchus McCosker

Paraletharchus McCosker 1974: 620. (Type species; *Letharchus pacificus* Osburn and Nichols, 1916, by original designation.)

DESCRIPTION: Anterior nostril tı
short, rounded at tip; median groo
side of snout absent; LL ossicles l
inders, not heavily fractionated (ı
22H and 22I); intermaxillary and vı
present; GO with a deep anterol
DFO above SO; dorsal fin elevated
sent; three supraorbital pores; neur
rounded, highest anterior to front
ture; hyoid arch stout, only slightly
EH-CH suture; HH separated from
row gap; branchiostegal rays nun
arch, distal rays along epihyal broad
UH a simple slender filament p
cartilaginous; pectoral girdle cont
and 2 rod-shaped elements; colc
uniform to mottled.

ETYMOLOGY: From the Greek
(para), near, and *Letharchus* (mas
lated genus.

DISTRIBUTION: Known from two
species, *P. opercularis* (Myers a
Galapagos endemic, and *P. paci*
and Nichols), ranging from Baja
Costa Rica.

REMARKS: As mentioned in the
Letharchus, the above-mentioned s
congeneric with *L. velifer*. Schult
(1960) placed *L. opercularis* in the
L. pacificus, however McCosker (19
ally recognized the Galapagos pop
tinct on the basis of the differenc
vertebral number (95% confiden
opercularis 172.7 - 176.6, *P. pac*
162.3).

Tribe Sphagebranchin

TYPE GENUS: *Caecula* Vahl 1794,
jective synonym of *Sphagebranchu*
(see following remarks).

DIAGNOSIS: Body (head and tr
moderately elongate, cylindrical, o
sed posteriorly; body either nearl
shorter than tail; snout pointed, o
depressed; lower jaw included; p
opens into mouth in most genera
ventral; median fins either very l
pectoral fin absent; tail tip sh
head pores well developed, tp[2] an
ally, and pop[4] sometimes preser

teeth conical, not caniniform, and
iserial; intermaxillary teeth sepa-
ap from those of vomer; neurocran-
e, generally depressed and truncate
orbit reduced; otic bulla moderately
loped; hyoid arch generally slender;
al rays few to numerous, generally
ciated with hyoid; gill arches re-
osent in most genera; intramuscular
and caudal transverse processes well
precaudal either nearly equal to or
ous than caudal vertebrae; colora-
ly uniform, or darker dorsally.

ncluded among the genera of the
hini are the most frustrating and
l of ophichthid taxa. Their nearly
ck of superficial characters has re-
istory of repeated lumping and split-
confusion stems from the inade-
misleading descriptions of the two
ic names, *Caecula* Vahl (1794) and
hus Bloch (1795). Gosline (1951:
ized the problem in stating that "the
nd consequently the limits, of the
la are agreed upon by no two au-
s I know."
 name Sphagebranchini is derived
son's (1838) family name Sphage-
Swainson's family name was subse-
ected (see page 10) long before
hus Bloch (1795) was shown to be
bjective synonym of *Caecula* Vahl
Böhlke and McCosker, 1975). The
 name Caeculidae has not appeared
hyological literature. In accordance
40 of the International Code of Zoo-
nenclature (1964), the family-group
gebranchini therefore has priority as
me, with *Caecula* as the type genus

Achirophichthys Bleeker

thys Bleeker 1865: 41. (Type species;
leeker 1865, by original designation.)

N (based on Bleeker, 1865, and
de Beaufort, 1916): Body stout,
ger than tail; snout pointed; eye
ior nostril not tubular, posterior nos-
to mouth; lips with one row of min-
ar papillae; DFO slightly behind GO;
eral to inferior; teeth conical, long
caniniform anteriorly and along vo-
al on vomer, biserial on maxilla.

ETYMOLOGY: From the Greek ἀχειρ (achir), without hands, and *Ophichthys*, (masculine), the amended spelling of *Ophichthus*.

DISTRIBUTION: A single western Pacific species.

REMARKS: An osteological diagnosis of *Achirophichthys* is not included in this study in that material of *A. typus*, the generic type, was unavailable. *A. kampeni* (Weber and de Beaufort), its sole described congener, is herein referred to *Lamnostoma*. Jordan and Davis (1891: 636) suggested that *A. typus* might be the young of *Brachysomophis crocodilinus*, but subsequent authors have neither accepted nor commented upon this action. Weber and de Beaufort (1916) considered *Achirophichthys* to be a subgenus of *Brachysomophis*. This too was ignored by most subsequent authors. Their description of *A. typus*, based on the type specimen, strongly indicates that it is congeneric with *A. kampeni*, which if true, would place *Achirophichthys* in the synonymy of *Lamnostoma*.

Apterichtus Duméril

Caecilia Lacépède 1800: 134. Preoccupied by *Caecilia* Linnaeus, a genus of Amphibia. (Type species; *C. branderiana* Lacépède 1800, by monotypy.)

Apterichtus Duméril 1806: 331. Also spelled *Apterichthys*, *Apterichthus*, *Apterichthe*, and *Apterichtes* by other authors. (Type species; *Muraena caeca* Linnaeus 1758, by monotypy.)

Typhlotes Fischer 1813: 81. A replacement name for *Caecilia* Lacépède, preoccupied.

Branderius Rafinesque 1815: 93. A replacement name for *Caecilia* Lacépède, preoccupied.

Ophisurapus Kaup 1856a: 52. (Type species; *O. gracilis* Kaup 1856, by monotypy.)

Ophisuraphis Kaup 1856b: 29. *Emend. pro Ophisurapus* Kaup 1856a.

Verma Jordan and Evermann 1896: 374. (Type species; *Sphagebranchus kendalli* Gilbert 1889, by original designation.)

?*Microrhynchus* Blache and Bauchot 1972: 728. Preoccupied by *Microrhynchus* Dejean 1821, a genus of lepidoptera, as well as mammalia (Jourdan 1834), crustacea (Bell 1835), aves (Lesson 1843) and vermes (Kepner 1935). (Type species; *Sphagebranchus foresti* Cadenat and Roux 1964, by original designation.)

DESCRIPTION: Body very elongate, cylindrical, and pointed at both ends; body and tail nearly subequal; snout pointed, sub-conical, grooved

and flattened on underside; lips without barbels; eye moderately developed; anterior nostril tubular, posterior nostril a horizontally ovate slit outside of mouth; GO ventral, converging forward; isthmus short; all fins absent; tp^{2} and pop^{4} presence variable among species; teeth pointed, uniserial in jaws, and largest at intermaxillary which is separated from those of vomer by a short gap; skull slightly depressed, sub-truncate to rounded posteriorly; orbit reduced; nasals and nasal cartilage developed; SOC short and blunt posteriorly; maxilla pointed posteriorly; opercular margins entire; suspensorium anteriorly inclined, jaw angle ca. 100°; PG slender, pointed and very reduced; hyoid arch slender, HH separated from CH by a gap; branchiostegal rays closely associated with hyoid; UH cartilaginous posteriorly; C_5 absent, UP_3-UP_4 separate; Cl broad, SCl reduced, Co and Sc absent; posterior trunk parapophyses with an anterior marginal projection (fig. 33).

ETYMOLOGY: From the Greek απτερόν (apteron), without fins, and (ichtus, more correctly written ichthys; masculine), fish.

DISTRIBUTION: From 10-12 described and valid species, represented in all tropical oceans. Böhlke (1968) provisionally reviewed the species of *Verma (=Apterichtus)*. The genus *Apterichtus* can be expanded to include: *Muraena caeca* Linnaeus (M), *Caecula gymnocelus* Böhlke (EP), *C. monodi* Roux (EA)*, *C. equatorialis* Myers and Wade (EP), *Sphagebranchus klanzingai* Weber (IP), *S. flavicaudus* Snyder (IP), *S. kendalli* Gilbert (WA), *Verma ansp* Böhlke (WA), *Ophisurapus gracilis* Kaup (EA)*, *Ophichthys anguiformis* Peters (EA)*, and possibly *Sphagebranchus foresti* Cadenat and Roux (EA)* and *Microrhynchus epinepheli* Blache and Bauchot (EA)*.

REMARKS: Blache and Bauchot (1972) recognized *Verma* as distinct from *Apterichtus* on the basis of a minor difference in posterior nostril location. Through the kindness of Enrico Tortonese I have examined a specimen of the Mediterranean *Apterichtus caecus*, and have concluded that it is clearly congeneric with the Atlantic and Pacific species previously referred to *Verma*. *Microrhynchus* Blache and Bauchot (1972) is based upon two species known only from the holotypes. Both were unavailable for study. Their sketchy description of the external morphology of the species, upon which the present study is based, does not provide characters which would allow their generic separation from *Apterichtus*, or possibly *Ichthyapu* *rorhynchus* prove to be a valid gen name will be required.

Caecula Vahl

Caecula Vahl 1794: 149. (Type spe *gera* Vahl 1794, by original desi *Sphagebranchus* Bloch 1795: 88. (*S. rostratus* Bloch 1795 = *Cae* Vahl 1794, by monotypy.)

DESCRIPTION: Body moderately e drical, compressed posteriorly; b nearly subequal; snout pointed, d broad dorsally, grooved and flatter side; eye moderate; anterior nos snout anteriorly, produced as a tu posterior nostril associated with entirely ventral, converging ant longer than isthmus, and with an duplication forming a deep pouch; behind GO; pop^{3} and tp^{2} present, teeth conical and uniserial, largest lary which is widely separated f vomer; skull depressed, broad, and teriorly; orbit extremely reduced nasal cartilage well developed; broad point posteriorly; maxilla elo posteriorly; coranoid process of ar ately enlarged; operculum well de operculum narrow and thin, their n suspensorium nearly vertical; h broad, expanded posterodorsally a strongly ridged; otic bulla weakly d slender, pointed at each end, and l hyomandibular by a posteromedi hyoid arch slender; HH separated a gap; branchiostegal rays nume unbranched, loosely associated wi ermost rays along epihyal slightl UH a slender filament posteriorl UP_3-UP_4 separated, anterior half c Cl, SCl, Sc and Co present.

ETYMOLOGY: A diminutive of th blind, regarded as feminine.

DISTRIBUTION: Two western Paci

REMARKS: Various species have be ly assigned to *Caecula* to such an has become a catch-all for most less ophichthids lacking pector (1964) redescribed the type of C. began the dissection of this con lage. Smith erred in presuming C.

pictum to be synonymous, and in
ric. Osteologically these genera are
eir coronoid processes, hyoid, gill
ostril conditions, but differ tren-
ir neurocrania.
l Bauchot (1972) placed the type
hagebranchus, *S. rostratus* Bloch, in
ke and McCosker (1975) considered
:ies of those genera to be conspe-
gested that the collection locality of
'river in Surinam") was erroneous.

Cirricaecula Schultz

ichultz 1953: 49. Type species; C.
chultz 1953, by original designa-

l: General characters those of *Ich-*
:rences include: body and tail near-
numerous cirri along edge of upper
ent barbel between the nostrils; an-
nearly flush with snout anteriorly,
iced as a tube posteriorly; GO en-
consisting of 2 parallel longitudinal
ı medial membranes; isthmus min-
l tp[2] present; otic bulla weakly de-
slender, pointed at each end; hyoid
HH separated from CH by a gap,
r filament posteriorly; C_3 ossified,
l; pectoral girdle reduced to a ven-
Cl pair which are broad and anteri-
l (fig. 19); CTP strongly developed.

From the Latin *cirrus*, tendril, and
nine), a related genus.

N: A single central Pacific species,
from the type series collected at
rshall Islands.

'hinus Weber and de Beaufort,
incertae sedis

Weber and de Beaufort 1916: 280.
es; *Sphagebranchus heyningi* Web-
original designation.)

: Body moderately elongate, cylin-
d at each end; body longer than
ointed, grooved on underside; eye
r nostril flush with snout; posterioı
eye, a long slit in upper lip; GO
:al; vertical fins low; tp[2] present(?),
).

Presumably from the Greek ἥμε
os), cultivated, and ῥινός
(rhinos; masculine in accordance with Item 30(a)(3) of the International Code of Zoological Nomenclature), nose.

DISTRIBUTION: Known from the type specimen, collected in deep water (69-91 meters) from Flores, Indonesia, and *H. opici* Blache and Bauchot (EA)*.

REMARKS: Species of *Hemerorhinus* were unavailable for study. Blache and Bauchot's (1972) redescription of the type species clarified several confusing aspects of the original description, particularly in correcting the mistaken intepretation of the nostrils and fin position. From their discussion however, I am unable to confidently find its placement within this tribe. On the basis of Blache and Bauchot's illustrations, the cephalic pore condition would indicate a similarity to the species of *Yirrkala*.

Ichthyapus de Barneville

Ichthyapus de Barneville 1847: 219. (Type species; *I. acutirostris* de Barneville 1847, by monotypy.)
Rhinenchelys Blache and Bauchot 1972: 718. (Type species; *Sphagebranchus ophioneus* Evermann and Marsh 1902, by original designation.)

DESCRIPTION: Body elongate, cylindrical, pointed at both ends; tail longer than body; snout pointed, depressed, and broad dorsally, grooved and flattened on underside; lips without barbels; eye small; anterior nostril flush with snout, posterior opens into mouth; GO entirely ventral, with a thin medial membrane, converging forward, isthmus small; all fins absent; tp[3] always and pop[4] usually present; teeth pointed, uniserial, and largest at intermaxillary which are separated from those of vomer by a gap; skull depressed, broad, and truncate posteriorly (fig. 8); orbit extremely reduced; nasals moderately, and nasal cartilage well developed; SOC moderately projecting posteriorly; maxilla elongate and pointed posteriorly; suspensorium nearly vertical; opercular margins entire, preopercle reduced; hyomandibular broad, expanded anteriorly and posterodorsally; otic bulla moderately developed; PG elongate and rectangular posteriorly, with a slender projection from the anterodorsal corner; hyoid thickened (not as slender as in related genera); HH separated from CH by a narrow gap; branchiostegal rays not numerous, slender and generally unbranched, closely asso-

ciated with hyoid, outermost rays along EH broadened basally; UH cartilaginous for posterior two-thirds; C_5 reduced (see Remarks), UP_3-UP_4 separate; Cl broad, SCl usualy absent, Sc and Co absent; posterior trunk parapophyses with an anterior marginal projection as in *Apterichtus* (fig. 33).

ETYMOLOGY: From the Greek ἰχθύς (ichthys), fish, and ἄπους (apous; masculine), without foot, presumably in reference to the lack of pectoral fins.

DISTRIBUTION: Circumtropical, with 6-7 valid species. Included are: *I. acutirostris* de Barneville (locality unknown)*, *Sphagebranchus vulturis* Weber and de Beaufort (=*Caecula platyrhyncha* Gosline) (IP), *S. ophioneus* Evermann and Marsh (WA), *Apterichthys selachops* Jordan and Gilbert (EP), and three undescribed eastern and western Pacific forms. *Incertae sedis: Sphagebranchus omanensis* Norman (IP).

REMARKS: The sharp-snouted finless species previously placed in *Sphagebranchus*, excluding the species of *Cirricaecula* and *Apterichtus* as herein defined, are referred to *Ichthyapus*. The generic type, *I. acutirostris*, is obviously congeneric with those species according to descriptions of the type made by de Barneville (1847, fide Fowler, 1936: 293), Kaup (1856b: 29) and Blache and Bauchot (1972: 718-728).

Blache and Bauchot (1972) differentiated *Rhinenchelys* from *Ichthyapus* on the basis of minor differences in nostril condition and intermaxillary tooth location. My examination of the osteology of *ophioneus*, the type of *Rhinenchelys*, indicates that it is congeneric with *selachops*, *vulturis*, and presumably *acutirostris*.

Nelson (1966a: table 1, figure 19) has described and illustrated the gill arch condition of *I. vulturis* (as *Caecula platyrhyncha*). The fifth ceratobranchial (C_5) is reduced and fused to the lower pharyngeal dermal tooth plate. I have found the gill arches of *I. ophioneus*, *I. vulturis*, and *I. selachops* to be similar in this condition. *Cirricaecula*, with a prominent C_5, appears intermediate between *Ichthyapus* and most Ophichthyini in this condition. The C_5 condition of the related genus *Apterichtus*, based on my examination of *A. flavicaudus*, is the most reduced in the group.

Lamnostoma Kaup

Lamnostoma Kaup 1856: 49 (23). (Type species; *L. pictum* Kaup 1856 = *Dalophis orientalis* McClelland 1844, by Jordan 1919b ;
viser.)

Anguisurus Kaup 1856: 50 (24). (Typ
A. punctulatus Kaup 1856 = Dalo
talis McClelland 1844, by monotypy.

DESCRIPTION: Body stout, cylindric
at each end; body slightly longer thar
pointed, its underside grooved; ey
moderate; anterior nostril flush alon
posterior rim produced, posterior no
associated with a pendulous flap; C
ca. equal to isthmus; DFO above or b
tp* and pop* absent; teeth slender, p
recurved, uniserial or biserial in jaw
intermaxillary and vomer largest a
spaced; neurocranium truncate
elongate and narrow, particularly alo
and interorbital region; orbit depres
and nasal cartilage moderately devel
present; maxillae moderately elonga
but not pointed posteriorly; coronoid
articular greatly enlarged; opercular s
erately developed, their margins enti
sorium anteriorly inclined, jaw angle
hyomandibular broad, expanded post
and strongly ridged; otic bulla well
PG slender, very reduced; hyoid sle
to branchiostegal rays in thickness, H
from CH by a broad gap, rays numero
unbranched, only the distal-most asso
hyoid, others terminate anteriorly be
slender UH, outermost rays along
broadened; gill arches reduced, C_5 a
UP_4 separate, B_1 cartilaginous except
tip which is ossified; Cl, SCl, and r
and Sc present; coloration generally
sally, a series of white spots across nap

ETYMOLOGY: From the Greek Λα
(lamna), a horrible anthropophagous
bugbear used by the Greeks to frigh
ory children (Jordan and Evermann,
and στόμα (stoma; neut

DISTRIBUTION: From the western P
visionally including four species.

REMARKS: *Lamnostoma* has been pla
cent authors in the synonymy of Ca
herein found to differ markedly in
osteological and morphological char
is consequently resurrected. The spe
genus are generally collected in fresl
are easily recognized by their slende
conspicuous white spotting on the

veral nominal species are included a, most of which fall into the syn- ·ientalis (McClelland). *Caecula min-* ıd Richardson and *C. taylori* Herre ıble to this genus. *Achirophichthys* ɔer and de Beaufort) is clearly a lts description, and recent refer- ng general morphological descrip- 1924; Nichols, 1955; La Monte, ese, 1964), concern large adults een collected in freshwater, each slender jaws and the head and of *Lamnostoma*.

ıinus Böhlke and McCosker

Böhlke and McCosker 1975: 5. es; *S. potamius* Böhlke and McCos- original designation.)

: General characteristics those of)ifferences include: Median fins but distinct, DFO ca. mid-trunk; op^{4} absent; LL ossicles with a short basisphenoid not elongate as in ompare Figs. 8 and 9); SOC re- ;ular series reduced, interopercle ercle reduced; branchiostegal rays ınched basally in some individuals, ated with hyoid, outermost rays ıdened basally; UH a slender ossi- posteriorly; C_5 absent; Cl broad l anteriorly, SCl absent, Sc and Co ık parapophyses lack an anterior . 33).

From the Greek στικτός ed or punctured, and ῥιν ɪ to rhinus, nominative case), nose, ɔ the nature of the anterior nostrils.

N: A single western Atlantic species, dal rivers in Brazil.

1971 Naercio Menezes sent the ɛs of eels from freshwater in Brazil. dentified as *Sphagebranchus rostra-* species known only from the type to have been from a "river in Suri- uent examination of the type speci- *:ula pterygera* and *Sphagebranchus* E. Böhlke found them to be based species, and the Brazilian specimens escribed genus and species (Böhlke ·r, 1975). My treatment (McCosker, *ıgebranchus* was therefore based on

Yirrkala Whitley

Yirrkala Whitley 1940: 410. (Type species; *Y. chaselingi* Whitley 1940 = *Sphagebranchus lumbricoides* Bleeker 1865, by original designation.)

Pantonora Smith 1964: 719. (Type species; *Ophichthys tenuis* Günther 1870, by original designation.)

DESCRIPTION: Body elongate, cylindrical, shorter than tail; snout conical, moderately developed, its underside grooved; eye moderate; anterior nostril in a short tube, posterior opens into mouth; GO ventral, longer than isthmus; DFO above or slightly behind GO; tp^{2} usually present, pop^{3} absent; teeth conical, pointed, nearly subequal, uniserial in jaws, those on vomer biserial anteriorly, separated from those of intermaxillary by a gap; skull not depressed, rounded posteriorly; orbit not strongly depressed; nasals and nasal cartilage moderately developed; SOC absent; maxilla pointed posteriorly; opercular series well developed, their margins entire; suspensorium anteriorly inclined, jaw angle ca. 100°; PG slender, pointed anteriorly; HH separated from CH by a short gap (HH absent in *Y. misolensis*); branchiostegal rays closely associated with hyoid; UH with a short projection posteriorly; C_5 absent, UP_3-UP_4 separate; pectoral girdle contains SCl, Cl, and reduced Co and Sc; posterior trunk parapophyses lack anterior marginal projections.

ETYMOLOGY: Named for Yirrkala, northern Australia, the type locality of the type species, masculine, in accordance with item 30(b)(ii) of the International Code of Zoological Nomenclature.

DISTRIBUTION: Contains approximately 12 species, from the eastern Atlantic, the Red Sea, and Indian and western Pacific Oceans. Included are: *Sphagebranchus lumbricoides* Bleeker, *Ophichthys tenuis* Günther, *Caecula maculata* Klausewitz, and an undescribed species from the Marquesas. *Incertae sedis: Sphagebranchus macrodon* Bleeker*, *S. gjellerupi* Weber and de Beaufort*, *S. kaupi* Bleeker, *Dalophis moluccensis* Bleeker*, *Ophichthys misolensis* Günther, *Muraena fusca* Zuiew*, and *Caecula natalensis* Fowler*.

REMARKS: The description of *Yirrkala* is so lacking in diagnostic characters as to preclude its proper placement, and consequently has been ignored by most recent authors. The only subsequent reference to *Y. chaselingi*, the generic

type, which I have encountered is that of Munro (1957) in which this species is placed in *Sphagebranchus*. I have examined and x-rayed the badly damaged and dessicated paratype of *Y. chaselingi*. The anterior nostrils, head pores, and gill openings are too badly damaged to allow accurate examination, however the dentition is well preserved and agrees well with Whitley's illustration. In his description, Whitley stated that *Y. chaselingi* and *Sphagebranchus lumbricoides* are congeneric, differing in the "position of dorsal origin, proportion of head to trunk, in having vomerine teeth largest, and other details of porportions and dentition." My comparison of the paratype of *Y. chaselingi* and specimens of *S. lumbricoides* from Vietnam (CAS 13969) and the Philippines (CAS reg. 1607) indicates that they are conspecific. The proportions, dorsal fin origins, dentition, and vertebral numbers (*Y. chaselingi* = 153, *S. lumbricoides* = 151,154) are not different.

Pantonora Smith (1964) is herein considered a synonym of *Yirrkala*.

Sphagebranchus kaupi and *Ophichthys misolensis* are provisionally referred to *Yirrkala*. *Y. kaupi* differs in having the major axis of its GO vertical. *Y. misolensis* differs in having basihyals fused to the ceratohyals, lateral line ossicles consisting of numerous short coils rather than small block-like segments, and lacking tp^2.

The external morphology of the species of *Hemerorhinus*, as described by Blache and Bauchot (1972), indicates that those species might be conspecific with the species within this complex. A comparative study of the type species of *Yirrkala*, *Hemerorhinus*, and *Pantonora* is clearly needed.

Tribe Bascanichthyini

TYPE GENUS: *Bascanichthys* Jordan and Davis, 1892.

DIAGNOSIS: Body (head and trunk) and tail moderately to extremely elongate, generally cylindrical, and compressed posteriorly in some genera; body either equal to or longer than tail; lower jaw included; posterior nostril opens into mouth; GO low lateral, crescentric, never entirely ventral; median fins generally low, DFO on head in most genera; pectoral fin absent or present as a minute flap in upper GO corner; head pores reduced, pop^3 and tp^2 absent; LL ossicles nearly continuous or separated by a short gap at pores; teeth conical, not caniniform; neurocranium variable in proportio terior shape; orbit generally reduc moderately to well developed; hy variable; branchiostegal rays num ated with the hyoid; gill arches re sent in most genera; IM bones, developed; precaudal vertebrae g numerous than caudal; coloratio form, or darker posteriorly.

Allips McCosker

Allips McCosker 1972: 116. (Typ *concolor* McCosker 1972, by ori tion.)

DESCRIPTION: Body elongate, most of its length; body much lo head markedly rugose; snout bl side grooved; eye small; anterior GO oblique, lateral, and less th length; median fins low, DFO in region; pectoral minute; caudal snout with numerous sensory ha nearly continuous; teeth small, co intermaxillary teeth largest, separa of vomer; skull sloping poste narrow slit; SOC weakly devel taper posteriorly; HH separated gap; branchiostegal rays numerou toral girdle reduced, only Cl, S Co (?).

ETYMOLOGY: From the Greek (allos), another, and line), a worm.

DISTRIBUTION: A single specie from the type specimen from Thai

Bascanichthys Jordan anc

Bascanichthys Jordan and Davis 1 species; *Caecula bascanium* J *Sphagebranchus teres* Goode by original designation.)

DESCRIPTION: Body elongate, compressed posteriorly; body lo head markedly rugose; snout sh its underside grooved; mouth sn anterior nostril tubular; GO ne low lateral, ≅ isthmus in lengt low, DFO on head; pectoral blunt; LL ossicles nearly continuo conical, uniserial in jaws, inte separated from those of vomer neurocranium sloping posteriorly

; and nasal cartilage moderately
nasals closely associated with the
ieir entire length; SOC absent;
slender, and pointed posteriorly,
: mid-vomer (fig. 16); opercular
ely developed, their margins en-
ium nearly vertical; otic bulla
veloped; PG pointed anteriorly;
from CH by a narrow suture;
rays numerous, often branched
g arch, the distal rays not broad-
JH either ossified or cartilaginous
reduced or absent, UP_3-UP_4 sep-
girdle consists of reduced Cl,

From *Bascanion* (diminutive, from
ασκανός, malignant),
ie for the black snake, and
's; masculine), fish.

All tropical oceans, with ap-
presently recognized species, in-
described eastern Pacific species
ind. Included are: *B. bascanoides*
hols (EP), *B. cylindricus* Meek and
, *B. panamensis* Meek and Hilde-
eciliae Blache and Cadenat (EA)*,
lache and Cadenat (EA)*, *B. paul-*
A), *B. pusillus* Seale (IP)*, Sphage-
Goode and Bean (WA), *S. longi-*
d Steindachner (IP)*, *S. scuticaris*
n (WA)*, *Callechelys myersi* Herre
's *filaria* Günther (IP)*. *Incertae*
ys *longissimus* Cadenat and Mar-
Ophichthys kirkii Gunther (IP)*.
nuis Tortonese, from New Guinea,
unior synonym of *B. longipinnis*.

species of *Bascanichthys* have
by Storey (1939), Ginsburg (1951)
c), and Blache and Cadenat (1971)
ic). The status of *Bascanichthys*
ered a junior synonym of *B. filaria*
: 316), is uncertain.

Caralophia Böhlke

ilke 1955: 1. (Type species; *C.*
hlke 1955, by original designa-

Body elongate, cylindrical, mod-
sed posteriorly; body longer than
onical, blunt from above, lacking
underside; eye moderate; anter-
ubular, a hole with lateral projections into it; GO ventral, converging forward, longer than isthmus; median fins low, DFO on head; tail tip pointed; LL narrowly separted at pores; teeth bluntly conical, uniserial in jaws and on vomer, intermaxillary teeth slightly larger, separated from those of vomer by a short gap; skull sloping posteriorly, depressed dorsally, orbit reduced; nasals stout and well developed, their margins entire, tightly joined to ethmoid; nasal cartilage well developed; frontals extend posteriorly to mid-parietals; SOC moderately developed, SO extends from mid-frontals posteriorly to a strong point; maxilla weak, slender, and pointed posteriorly; opercular series developed, their margins entire; suspensorium posteriorly inclined, jaw angle ca. 100°; otic bulla moderately developed; PG broad centrally, closely associated with maxilla anteriorly; hyoid stout, HH fused to CH; branchiostegal rays numerous, along arch, and often branched basally; distal rays along EH broadened basally; UH reduced to a well ossified basal plate with a posterior cartilaginous filament; tooth plates reduced, UP_3-UP_4 fused; pectoral girdle reduced to a Cl and fragments of a SCl, Sc, and Co.

ETYMOLOGY: From the Greek καρα, head, and λοφία (lophia; feminine), a mane, in reference to the anterior dorsal fin origin.

DISTRIBUTION: A single western Atlantic species, extending from the Bahamas to the lesser Antilles and Panama.

Dalophis Rafinesque

Dalophis Rafinesque 1810a: 68. (Type species; *D. serpa* Rafinesque 1810a = *Sphagebranchus imberbis* De la Roche 1809.)
Pterurus Rafinesque 1810b: 59. (Type species; *P. flexosus* Rafinesque 1810b = *Sphagebranchus imberbis* De la Roche 1809, by monotypy.)
Scytallurus Duméril 1856: 199. (Type species; *Sphagebranchus imberbis* De la Roche 1809, by monotypy.)
Pelia Bleeker 1863: 128. (Type species; *P. cephalopeltis* Bleeker 1863.)

DESCRIPTION: Body moderately elongate, cylindrical, slightly compressed posteriorly; tail longer than body; snout sub-conical, grooved on underside; eye small; anterior nostril tubular; GO low on body, extending onto venter, its length ≅ isthmus; vertical fins low, DFO well behind GO; pectoral fin rudimentary if present; tail tip blunt; LL ossicles widely separated at

pores; teeth conical, uniserial, intermaxillary teeth separated from those of vomer by a gap; skull subtruncate posteriorly, orbit depressed; nasals well developed; SOC weakly developed; maxilla tapers posteriorly; suspensorium nearly vertical; HH separated from CH by a gap; UH ossified posteriorly; gill arches stout, H_3 ossified, C_5 a slender ossified rod, UP_3-UP_4 separate; pectoral girdle reduced, only a Cl and SCl present.

ETYMOLOGY: The significance of the prefix Is not obvious, but possibly derived from Dalmatia, then a country on the east side of the Adriatic Sea, and ὄφις (ophis; masculine), a snake.

DISTRIBUTION: Five eastern Atlantic and Mediterranean species are presently recognized, including: *D. boulengeri* Blache and Bauchot (EA)*, *D. multidentatus* Blache and Bauchot (EA)*, *D. obtusirostris* Blache and Bauchot (EA)*, *Pelia cephalopeltis* Bleeker (EA)*, and *Sphagebranchus imberbis* De la Roche (M).

REMARKS: Blache and Bauchot (1972) have recently expanded *Dalophis* to include *Pelia* and five nominal species. Their finding (p. 746) that the pectoral fin, though generally absent, may be represented by a "miniscule filament" is in agreement with Lozano Rey's (1947, p. 546). Through the kindness of Enrico Tortonese I have been able to examine and partially dissect a specimen of *Dalophis imberbis*. A complete osteological preparation, however, was impossible.

Dalophis has been summarily synonymized with *Caecula* by previous authors. Its general facies (physiognomy, low median fins, and body depth and taper) and certain osteological features (dentition, pectoral girdle, and anterior trunk vertebrae) suggest a relationship with *Ethadophis* and *Leptenchelys*, genera restricted to the eastern Pacific. The gill arch skeleton and body/tail proportions are typically ophichthin, and for that reason, *Dalophis* is placed in the Bascanichthyini with reservations.

Ethadophis Rosenblatt and McCosker

Ethadophis Rosenblatt and McCosker 1970: 498. (Type species; *E. byrnei* Rosenblatt and McCosker 1970, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical anteriorly, becoming compressed posteriorly; body equal to or slightly longer than tail; snout rounded, conical from above; eye small; anterior nostril tubular; GO low on body, extending onto venter, their length
vertical fins low, DFO before GO;
fleshy in one species; LL ossicle
pores; teeth conical, uniserial,
teeth separated from those of vo
skull subtruncate posteriorly, or
nasals well developed; SOC mo
oped, pointed as in *Bascanichthy*
ers posteriorly; suspensorium nea
separated from CH by a gap; bra
numerous, slender and along hyo
posteriorly; UP_3-UP_4 separate; pe
duced, only a Cl, SCl, and Co (?)
by radiograph.

ETYMOLOGY: From the Greek
(ethas), customary or ordinary, a
(ophis; masculine), serpent.

DISTRIBUTION: Two species, *E.*
blatt and McCosker and *E. mer*
and McCosker, known only from
mens from Baja California, Mexico

Gordiichthys Jordan and

Gordiichthys Jordan and Davis 1
species; *G. irretitus* Jordan a
by original designation.)

DESCRIPTION: Body extremely
drical, much longer than tail; sno
moderate; GO low lateral; DFC
teeth conical, recurved, and unise

ETYMOLOGY: From *Gordius*,
worm, named after Γόρδ
whose complicated knot was cu
and ἰχθύς (ichthys;

DISTRIBUTION: Known from a si
western Atlantic species.

REMARKS: The above descripti
Jordan and Davis (1891) and Gi
that material of *G. irretitus*, the t
unavailable for study. *Gordiichth*
scribed by J. E. Böhlke (personal
G. springeri Ginsburg, its sole
gener, is a species of *Callechelys*
and McCosker, 1970, and McCo
blatt, 1972).

Leptenchelys Myers and

Leptenchelys Myers and Wade
species; *L. vermiformis* Myers
by original designation.)

l: Body elongate, cylindrical, slightly
ɔosteriorly; body longer than tail;
subconical; top of head and snout
numerous papillae; eye small; an-
tubular; GO low lateral, crescentic,
ƆFO on head; median fins conflu-
tail tip; teeth weak, pointed, uni-
sloping posteriorly, orbit reduced;
not projecting posteriorly; suspen-
iorly inclined, jaw angle ca. 100°;
ender, HH separated from CH by a
branchiostegal rays slender, appear
aph to lie along hyoid; pectoral
d, only SCl and Cl visible in radio-

: From the Greek λεπτός
, and ἔγχελυς (enchelys;
ne or masculine, treated as mascu-

N: A single species, known only
pe specimen from Playa Blanca,
Rica.

ıis poorly known genus is provision-
to the Bascanichthyini. The generic
ntly uncollected since the capture
m type specimen, was examined and
for the purpose of this study. Its
a bascanichthyin is based on the
anchiostegal rays which appear to
ıyoid, the posteriorly sloping neuro-
low unconstricted gill openings,
pore configuration. Caudal fin rays
ın the type specimen, but are more
ıped than any myrophine's.
ys has had an erratic history. Origi-
in the Echelidae on the basis of its
dal fin (Myers and Wade, 1941), it
nonymized with *Muraenichthys* by
Woods (1949), re-erected and ex-
chultz, et al. (1953), and finally, re-
a single species (McCosker, 1970)
rkedly from *Muraenichthys* and re-
a. *Leptenchelys tenuis* Tortonese
New Guinea is a species of *Bascan-*
:h is possibly synonymous with *B.*
described from Samoa. My exami-
holotype of *L. tenuis* indicates that
verlooked the rudimentary pectoral
developed in *B. longipinnis* accord-
(1939). The tail tip of *L. tenuis* is
shy, but not unlike that of other
ıscanichthys.

Phaenomonas Myers and Wade

Phaenomonas Myers and Wade 1941: 77. (Type species; *P. pinnata* Myers and Wade 1941, by original designation.)

DESCRIPTION: Body elongate, cylindrical, much longer than tail; head markedly rugose; snout blunt, grooved ventrally; eye minute; anterior nostril tubular; GO low lateral, oblique and elongate, ≅ isthmus; DFO mid-head, low, ending in anterior trunk region; anal fin absent; teeth small, conical, uniserial, intermaxillary teeth largest, separated from those of vomer; skull sloping posteriorly, orbital foramen a narrow slit; nasal cartilage weak; SOC weakly developed; maxilla tapers potseriorly; opercular series reduced, all but opercle serrated at margin; suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG free and tapering anteriorly; HH separated from CH by a gap; branchiostegal rays numerous, slender and along hyoid; UH club-shaped, cartilaginous posteriorly; pectoral girdle reduced, only SCl, Cl, and a thin Co (?); IM bones, ribs, and CTP weakly developed.

ETYMOLOGY: Presumably from the Greek φαίνω (phainos), to show, and μονάς (monas; feminine), single or alone, in reference to the unique dorsal fin condition.

DISTRIBUTION: Two described species, *P. pinnata* Myers and Wade ranging from the Gulf of California to Colombia, and *P. cooperae* Palmer, ranging from Hawaii to the western Indian Ocean (McCosker, In Press).

Tribe Ophichthini

TYPE GENUS: *Ophichthus* Ahl, 1789

DIAGNOSIS: Body (head and trunk) and tail moderately elongate, cylindrical anteriorly, generally compressed posteriorly; body usually shorter than tail; snout conical or subconical; lower jaw usually included; anterior nostril generally tubular; posterior nostril opens into mouth in most genera; gill openings lateral, their major axis vertical, crescentic, about equal to, less than, or longer than isthmus; median and pectoral fins present; tail tip sharply to bluntly pointed; tp[3] and pop[4] absent; dentition variable, including caniniform and molariform conditions; neurocranium moderately elongate; orbit well developed; otic bulla moderately to well developed; hyomandibular moderately to strongly ridged;

opercular series well developed, margins entire; gill arches well developed, C_5 present in many genera; pectoral girdle generally well developed; intramuscular bones, ribs, and caudal transverse processes well developed; coloration variable.

Aplatophis Böhlke

Aplatophis Böhlke 1956b: 1. (Type species; *A. chauliodus* Böhlke 1956b, by original designation.)

DESCRIPTION: Body stout, not elongate, laterally compressed posteriorly; body slightly longer than tail; jaws elongate, the lower projecting beyond the upper; eye small; posterior nostril in a short tube before and beneath eye; GO vertical, lateral and elongate, less than isthmus; DFO behind pectoral tips; tail tip blunt; pop[3] absent, median head pores absent although frontal commissure and supratemporal canal are present; LL ossicles widely separated at pores; anterior teeth of both jaws excessively developed as long fanglike canines extending far outside mouth when closed, jaw teeth biserial, those of vomer few and uniserial and continuous with those of intermaxillary; skull subtruncate posteriorly, orbit large, eyeball displaced anteriorly; PO ossicles weak, not fused as a strut to maxilla; nasals extremely reduced to a short and slender canal, nasal cartilage absent; frontal midline elevated anteriorly forming a sharp ridge extending to SO; SOC absent, SO anteriorly contacts frontals and separates parietals; maxilla elongate, rounded posteriorly; opercular series developed, subopercle scythe-shaped, preopercle enlarged; suspensorium posteriorly inclined, jaw angle ca. 80°; hyomandibular ridged and elongate posterodorsally for muscle attachment; otic bulla well developed; PG broad posteriorly, free and terete anteriorly, HH separated from CH by a gap; branchiostegal rays slender, rays of EH joined basally; UH a spike posteriorly; C_5 ossified, UP_3-UP_4 separate, B_{2-4} absent; pectoral fin moderately developed, girdle well developed, Sc and Co large, actinosts absent (fig. 19F); caudal vertebrae fewer than precaudal; coloration nearly uniform, slightly darker dorsally.

ETYMOLOGY: From the Greek ἄπλατος (aplatos), unapproachable, and ὄφις (ophis; masculine), serpent.

DISTRIBUTION: Known from a single trans-Atlantic species.

Brachysomophis Kaup

Brachysomophis Kaup 1856: 45 (9
cies; *B. horridus* Kaup 1856 = Op
odilinus Bennett 1833, by monotyp

DESCRIPTION: Body cylindrical, elongate, longer than tail; snout ve blunt; jaws elongate, with lower jaw truding; eye moderate; a conspicuo depression exists in the postorbit some species; lips with numerous s terior nostril in a very short tube, po into mouth; GO low lateral, cresc than isthmus; DFO well behind pect tip sharply pointed; pop[3] absent; separated at pores; teeth strong, c lary biserial, dentary uniserial, tho uniserial, large, and widely separat but continuous with those of interm subtruncate posteriorly, orbit redu most postorbital with a broad an forming posterior margin of orbit, ti to smaller postorbitals to form a n (fig. 15); nasals and nasal cartila duced; SOC absent, SO broad post illa elongate, tapering posterior series well developed, margins sli suspensorium nearly vertical; h ridged; otic bulla well develope posteriorly, tapering to a fine poi hyoid arch slender, HH separated a gap; branchiostegals slender and closely associated with hyoid; UH teriorly; C_5 ossified, UP_3-UP_4 sepa fin and girdle reduced, SCl and act SC reduced; caudal vertebrae few caudal; coloration uniform or dark

ETYMOLOGY: From the Greek β (brachys), short, σῶμα (and ὄφις (ophis; mascu

DISTRIBUTION: Known from fou western Pacific and a single eastern cies. Günther's (1870) report of B from the Galapagos Islands was roneus (Rosenblatt et al., 1972).

REMARKS: The species of *Brachy* clearly in need of revision (Schultz, 1962) but I am lacking the materia required comparisons. *Brachysomo* Blache and Saldana (1972) was rece from Senegal. The Pacific species o *phis* include: *Ophisurus cirrhoch*

is Bennett*, *Brachysomophis hen-* and Snyder, and *B. sauropsis* ıst three nominal species are quite ːrhaps conspecific. *B. cirrhocheilos* ıose species in apparently lacking l depression, in its longer pectoral ' banded coloration (fide Deraniya- ıe neurocranium and suspensorium ıwi were illustrated by Gosline

on of the fused postorbital strut in ıchysomophis is functionally con- hat of *Ophichthus zophochir*, how- 'd, dorsal-most postorbital of *B.* nger than the second, and enlarged ɔrm a cup that braces the eye.

Cirrhimuraena Kaup

Kaup 1856; 51 (27). (Type species; Kaup 1856, by monotypy.)
rdan and Evermann 1905: 83. (Type *'icrodonophis macgregori* Jenkins ginal designation.)
Whitley 1944: 261. (Type species; *calamus* Günther 1870, by original)
Günther 1870, *sic* Rosenblatt and 970: 496, *lapsus pro Calamuraena* 4.

: General characteristics those of)ifferences include: DFO generally bove GO; pectoral fin moderately loped; upper lip with numerous ɟenerally present; teeth conical, not enlarged, often multiserial in vomer, those of intermaxillary and tinuous; skull subtruncate posteri- than in *Ophichthus*); PO strut ab- frontal crests weakly developed; ɟate posteriorly; otic bulla not oped; actinosts absent, or 1-2; col- m, often darkened dorsally.

From the Latin *cirrus* (cirrh is a y common form of *cirr*, mistakenly be from the Greek κιρρός ıing yellow or tawny), tendril, and nus of muraenid eels.

ɬ: An Indo-Pacific and Red Sea . 9 valid species.

rrhimuraena is broadly defined to ·s that have been referred to *Cala-* *'enkinsiella*. Subgeneric lines within *Cirrhimuraena* may be separated on an external morphological basis in the following manner:

Mandibular and vomerine teeth uniserial; pop^3 absent (not determined for all species) .... subgenus *Jenkinsiella*

Mandibular and vomerine teeth multiserial; pop^3 present (not determined for all species) .... subgenus *Cirrhimuraena*

The subgenus *Jenkinsiella* Jordan and Evermann includes *Microdonophis macgregori* Jenkins, *Ophichthys playfairii* Günther*, and may include *Jenkinsiella oliveri* Seale* and *J. inhacae* Smith*. The remaining species belong in the subgenus *Cirrhimuraena* Kaup (which includes *Calamuraena* Whitley), including: *Cirrhimuraena chinensis* Kaup, *C. taeniopterus* Bleeker, *C. paucidens* Herre and Myers (=*C. chinensis*?), *Ophichthys calamus* Günther, and *Ophisurus cheilopogon* Bleeker*. *Cirrhimuraena* may merit further generic division, particularly if confirmed by an osteological study of all the included species.

Nelson's (1966a: 395) description of the fifth ceratobranchial of *C. macgregori* as having "the proximal portion of C_5 cartilaginous . . . (and) the distal portion extending posteriorly as a thin filament of cartilage" does not agree with my findings on available specimens. In them the distal portion is well ossified. Gosline (1951a: fig. 6) has illustrated the neurocranium and suspensorium of *C. macgregori*.

Echelus Rafinesque

Echelus Rafinesque 1810a: 63. (Type species; *E. punctatus* Rafinesque 1810a = *Muraena myrus* Linnaeus 1758, by Bleeker 1864 as first reviser.)
Myrus Kaup 1856: 53 (31). (Type species; *M. vulgaris* Kaup 1856 = *Muraena myrus* Linnaeus 1758, by monotypy.)

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: DFO before pectoral tips; median fins continuous around tail; head pores reduced, pop^3 present, temporal, postorbital, and interorbital pores absent; cephalic surface sensory pores well developed; teeth multiserial, small, nearly granular, intermaxillary teeth continuous with those of vomer; PO strut absent, but a cartilaginous antorbital strut present in *E. myrus*; SO and frontal crests moderately developed; maxilla slender posteriorly; branchiostegal rays few; coloration nearly uniform, darker dorsally.

ETYMOLOGY: From the Greek ἔγχελυς (enchelys, considered either feminine or masculine, regarded as masculine by Rafinesque, Kaup, and Bleeker), eel.

DISTRIBUTION: Known from a shallow and a deep-water species from the Mediterranean and eastern Atlantic, respectively, *E. myrus* (Linnaeus) and *Myrus pachyrhynchus* Vaillant.

REMARKS: The osteology of the species of *Echelus* indicates that they are closely related to species of *Ophichthus*, with particular similarities evidenced in the hyoid arches, gill arches, and neurocrania. The conspicuous presence of a caudal fin led previous workers to consider *Echelus* to belong to a family or subfamily separate from *Ophichthus*. The tail fin is clearly a superficial condition that does not merit such suprageneric separation, and thus the family name Echelidae is referred to the synonymy of the Ophichthidae, and the subfamily Echelinae to that of the Ophichthinae.

The species of *Echelus* are easily separable from other ophichthins on the basis of two characters, the presence of extremely visible caudal fin rays, and the head pore reduction. The produced caudal fin appears to be a primitive retention of an ancestral conditon, although the hard-pointed tail tip characteristic of other ophichthines was probably achieved early in the evolution of the subfamily. The absence of the temporal, postorbital, and interorbital pores (as noted by Gosline, 1952) probably reflects the loss of these openings, in that the cephalic lateralis canals and frontal commissures of *E. myrus* (Allis, 1903: figs. 5-8, and personal observation) and *E. pachyrhynchus* (personal observation) have been retained. The antorbital cartilaginous strut of *E. myrus*, as identifed by Gosline (1952), is not present in *E. pachyrhynchus* and does not appear ot be an important indicator of phylogeny. Gosline (1952: 133) suggested that "*Echelus myrus* appears, despite specializations, to be by far the most primitive (or generalized) ophichthid known. In fact, to a considerable degree it fills in the gap between the Ophichthidae and the Congridae." I concur with Gosline in considering *Echelus* to be a very generalized (primitive) ophichthid, however its gill arch reduction, labial posterior nostril, and hyoid apparatus suggest that it is well separated from any congrid-like ancestor.

The neurocranium of *Echelus myrus* has been discussed and illustrated by Storms (1896, as *Myrus vulgaris)* and by Gosline (1952), a external morphology of *E. myrus* and *E. rhynchus* by Blache (1968).

Echiophis Kaup

Echiophis Kaup 1856a: 46. (Type species; *urus intertinctus* Richardson 1844b, by typy.)

Echiopsis Kaup 1856b: 13. *Emend. pro Ech* Kaup 1856a.

Crotalopsis Kaup 1860: 12. Also spelled *C pis, Crotalophis*, by other authors. (Typ cies; *C. punctifer* Kaup 1860, by monoty

Macrodonophis Poey 1867: 251. (Type sp *Conger mordax* Poey 1861, by monotypy

DESCRIPTION: Body cylindrical, mod elongate, laterally compressed posteriorly; shorter than tail; snout short, subconical, s constricted near tip; jaws elongate and equal; eye moderate; posterior nostril in a tube before and beneath eye; GO vertical, and elongate, ≅ ishtmus; DFO behind p tips; tail tip blunt; pop^3 present; LL ossicle arated at pores; teeth strong, pointed a serial, largest anteriorly in jaws and on et those of intermaxillary and vomer biseri nearly continuous; skull subtruncate poste preorbital region reduced, orbit large; PO to skull and maxilla, forming a strut; slender, nasal cartilage reduced or absent absent; maxilla elongate, rounded poste toothed along most of its length; opercula gins entire, subopercle scythe-shaped; s sorium posteriorly inclined, jaw angle ca hyomandibular ridged and elongate poste sally for muscle attachment; otic bulla w veloped; PG broad posteriorly, free and anteriorly; hyoid arch slender, HH sep from CH by a narrow gap; branchiosteg numerous, all slender, unbranched, and hyoid; UH a spike posteriorly; C_5 ossified UP_4 fused; pectoral girdle and fin develop and Co large, actinosts present; caudal ver slightly more than precaudal; coloration ally strongly spotted.

ETYMOLOGY: From the Greek ἔχις (echis), viper, and ὄφις (ophis; line), serpent. Kaup emended the suffix to ις (opsis), appearance.

DISTRIBUTION: A largely New World gen taining 3-5 Atlantic and Pacific species. In are: *Ophisurus intertinctus* Richardson (W

Mystriophis cruetzbergi Cadenat), *Conger*
r Poey (WA), *Crotalopsis punctifer* Kaup
ınd an undescribed eastern Pacific species
; from the Northern Gulf of California to
ı. *Incertae sedis: Mystriophis blastorhinos*
wa (WA).

:KS: The species of *Echiophis* form a dis-
complex within the Ophichthini, and are
t to separate at the specific level. The At-
ipecies are separable from each other on
iis of spot size, yet a continuous grade is
present. Opinions as to the distinctiveness
Atlantic species have been presented (Jor-
d Davis, 1891; Springer and Allen, 1932;
rg, 1951) yet a conclusive study is still
. The morphology of eastern Atlantic
ens of *E. intertinctus* is described by
(1971).

Elapsopis Kaup

ris Kaup 1856: 45 (9). Emended to *Elaps-*
; by other authors. (Type species; *Ophi-*
; *versicolor* Richardson 1844, by mono-
)
hichthys Whitley 1951: 392. Described as
ıbgenus of *Malvoliophis* Whitley 1934.
e species; *Ophichthus cyclorhinus* Fraser-
ner 1934, by original designation.)

IPTION: General characteristics those of
ıus. Differences include: anterior nostril
ort tube, its rim flared distally; DFO above
htly before GO; pectoral fin reduced, $\cong$
ngth; vomerine teeth present; opercular
fringed; C_5 ossified; actinosts of pectoral
present.

ILOGY: From the Latin *elaps* (masculine),
e, and *opis*, an erroneous spelling of the
ὄψις (opsis), meaning appearance.

BUTION: Included are two, probably con-
:, species, from Australia, Lord Howe Is-
ınd the southern Caroline Archipelago.

KS: This genus is provisionally recognized
inct from *Leiuranus* on the basis of the
ntly secondary ossification of the fifth
ranchial and the presence of actinosts.
casional presence of 1-2 vomerine teeth
imens of *L. semicinctus* approaches the
ın of certain specimens of *E. versicolor*
cyclorhinus. Further investigation may re-
he recognition of *Elapsopis* as a subgenus
anus.

Evips McCosker

Evips McCosker 1972: 113. (Type species; *E. percinctus* McCosker 1972, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout blunt, conspicuously papillate; lower jaw included; eye large; DFO behind GO; pectoral fin minute; tail tip pointed; pop^3 absent; LL ossicles continuous, but heavily fractionated; teeth pointed, uniserial, except those of maxilla which are biserial, largest at intermaxillary which are continuous with those of vomer; skull subtruncate posteriorly, orbit large; SOC pointed posteriorly; maxilla moderately produced, slender posteriorly; suspensorium nearly vertical, jaw angle ca. 95°; hyoid stout, HH separated from CH by a gap; branchiostegal rays numerous, all slender and associated with hyoid; UH a spike posteriorly; C_5 present, UP_3-UP_4 separate; pectoral girdle reduced to a slender Cl (SCl not visible in radiograph), actinosts absent; caudal $\cong$ precaudal vertebrae; coloration strong banded.

ETYMOLOGY: From the Greek εὖ (eu, latinized to ev for euphony before a vowel), good, and ἶψ (ips; masculine), a worm.

DISTRIBUTION: A single species known only from the type specimen from the Southern Caroline Archipelago.

Leiuranus Bleeker

Leiuranus Bleeker 1853a: 24. (Type species; *L. lacepedii* Bleeker 1853a = *Ophisurus semicinctus* Lay and Bennett, by monotypy.)
Stethopterus Bleeker 1853a: 24. (Type species; *Ophisurus (Sphagebranchus) vimineus* Richardson 1844a = *Ophisurus semicinctus* Lay and Bennett 1839, by monotypy.)
Machaerenchelys Fowler 1937: 85. (Type species; *M. vanderbilti* Fowler 1937 = *Ophisurus semicinctus* Lay and Bennett 1839, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body and tail subequal; snout conical, flattened and grooved on underside; lower jaw included; eye moderate; anterior nostril in a short tube, posterior along lip margin; GO vertical, crescentic, shorter than isthmus; median fins low, expanded before tail tip; DFO above GO; pectoral fin moderately developed; tail tip sharply pointed;

pop^3 absent; LL ossicles narrowly separated at pores; teeth small, recurved, uniserial, absent from vomer or 1-2 small teeth; neurocranium subtruncate posteriorly, orbit large; PO strut absent; nasals and nasal cartilage moderately developed; frontal-parietal ridge and SOC developed; maxilla short, articulated ca. mid-vomer; maxillae closely apposed anteromedially (but not abutting as per Gosline, 1951a: 301); suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG slender, braced posteriorly by hyomandibular, pointed anteriorly; HH separated from CH by a short gap; branchiostegal rays numerous, slender (distal-most broadened slightly), unbranched, and associated with hyoid (except for innermost rays); UH split anteriorly (less so than in *Phyllophichthus),* produced posteriorly as a spike; gill arches weak, C_5 absent, anterior half of H_1 ossified; pectoral girdle reduced, actinosts absent; precaudal vertebrae more numerous than caudal; coloration strongly banded.

ETYMOLOGY: From the Greek λεῖος (leios), smooth, and οὐρανός (ouranos; masculine), sky, in reference to the toothless vomer.

DISTRIBUTION: A single species, widespread in the central and western Pacific and Indian oceans.

REMARKS: Gosline (1951a: fig. 4) has illustrated the neurocranium and suspensorium of *L. semicinctus.*

Malvoliophis Whitley

Malvoliophis Whitley 1934: 154. (Type species; *Bascanichthys hemizona* Ogilby = *Ophichthys pinguis* Günther 1872, by original designation.)

DESCRIPTION: Body elongate, subcylindrical, laterally compressed; body shorter than tail; snout developed, subconical, a short groove on underside; lower jaw included; eye large; anterior nostril tubular; DFO before GO; pectoral fin moderately developed; pop^3 absent; LL ossicles widely separated at pores; teeth conical, not sharply pointed, unserial in jaws, largest at intermaxillary which are widely separated from those of the vomer; skull subtruncate posteriorly, orbit large; PO strut absent; maxilla elongate, slender posteriorly; opercular series weakly developed; suspensorium nearly vertical, jaw angle ca. 95°; otic bulla moderately developed; PG broad posteriorly, slender anteriorly; hyoid slender, HH separated from CH by a suture; branchiostegal rays numerous, slende slightly flattened, the anteriormost ray enlarged; UH broad anteriorly, a short posteriorly; C_5 weakly ossified (cartilagi UP_3-UP_4 fused; pectoral girdle reduced, Sc, Co, and actinosts; caudal vertebrae numerous than precaudal; coloration banded and spotted.

ETYMOLOGY: From Malvolio, Lady (steward in Shakespeare's *Twelfth Nigh* ὄφις (ophis; masculine), serpen banded coloration of *M. pinguis,* the (type, suggests the cross-gartered legs and socks worn by Malvolio (G. P. Whitley, p(communication).

DISTRIBUTION: A single species, reporte(southern Queensland, New South Wale Lord Howe Island.

Myrichthys Girard

Myrichthys Girard 1859: 58. (Type speci *tigrinus* Girard 1859, by monotypy.)

Chlevastes Jordan and Snyder 1901: 867. species; *Muraena colubrina* Boddaert 1; original designation.)

DESCRIPTION: General characteristics th *Pisodonophis* and *Ophichthus.* Differen(clude: snout short (for an ophichthin), from above; DFO well before GO; pect(short, broad-based (fig 34); pop^3 absent, molariform or granular, multiserial on ja\ vomer, largest at intermaxillary, which a rowly separated from those of vomer; P(absent; maxilla elongate, slender post(teeth of pharyngeal plates generally sm; pavement like; pectoral girdle reduced, duced, Sc and actinosts absent; coloration spotted, banded, or both.

ETYMOLOGY: From the Greek μύρ (myrus), eel, and ἰχθύς (i(masculine), fish.

DISTRIBUTION: A circumtropical genus c(including seven valid species. The genus (expanded to 12 should certain insular (tions of *M. maculosus* and *M. xystrurus* p be distinct. Included in *Myrichthys* a(*bleekeri* Gosline (a substitute name for *surus fasciatus* var. *semicinctus* Bleeker, cupied) (IP), *M.* sp. (EP), *Muraena ac(* Gronow (WA), *M. colubrina* Boddaert (*maculosa* Cuvier (IP), *Pisodonophis oculat(*

Ophisurus pardalis Valenciennes (EA)*, *hichthys xystrurus* Jordan and Gilbert (EP) narks).

KS: *Muraena tigrina* Rüppell (1826), de- from the Red Sea, is currently placed in onymy of *Myrichthys maculosus* (Cuvier). ates a homonymy with the eastern Pacific *hys tigrinus* Girard (1859), the type spe- the genus. *Myrichthys xystrurus* (Jordan bert, 1882) is the next available name for ern Pacific species.

genera *Pisodonophis* and *Myrichthys* are ts from a generalized *Ophichthus*-like an- Within the examined species of *Pisodon-* trend in characters is evident, with *P.* *rus* the most *Ophichthus*-like and *P.* *us* the most *Myrichthys*-like (the char- owever, are discontinuous enough to al- neric separation). These trends include: nsformation from pointed to molariform n; the advancement of the DFO; the re- in length and basal broadening of the l fin; and the reduction of the coracoid of the scapula.

' (1949) has pointed out that the type of *M. tigrinus* is properly Adair Bay, Mex- : Oregon.

ne (1951a) has illustrated the neurocran- ertebrae, gill arches, and pectoral girdle *aculosus.*

Mystriophis Kaup

phis Kaup 1856: 45 (10). (Type species; *surus rostellatus* Richardson 1844, by otypy.)

PTION: Body cylindrical, moderately e, laterally compressed posteriorly; body than tail; snout short, subconical, con- near tip; jaws elongate, the lower slightly ; eye moderate; posterior nostril at edge er lip, covered by a flap; GO vertical, lat- d elongate, ≅ isthmus; DFO above or be- ectoral tips; tail tip blunt; pop³ absent, ry cephalic pores well developed; LL separated at pores; teeth strong, pointed, largest anteriorly in jaws and on eth- ntermaxillary and uniserial vomerine teeth continuous; coloration nearly uniform, d dorsally.

.OGY: From the Greek μυστρίον n), a spoon, and ὄφις (ophis; ne), serpent, in relation to the snout f *M. rostellatus*, the generic type.

DISTRIBUTION: Two eastern Atlantic and one Japanese species are provisionally placed in *Mystriophis* (see following Remarks).

REMARKS: Specimens of *Mystriophis* were unavailable for osteological examination, therefore the above description was prepared from Blache (1971). The genera *Mystriophis* and *Echiophis* have been separated by recent authors (Ginsburg, 1951; Kanazawa, 1963; Rosenblatt and McCosker, 1970; Blache, 1971) on the basis of the snout shape and vomerine dentition. *M. rostellatus* Richardson and *M. crosnieri* Blache, from the eastern Atlantic, are undoubtedly congeneric and appear to be recently derived from an *Ophichthus*-like ancestor (evidenced in the pop³ absence, secondary cephalic pore development, moderate snout length, and body coloration). The species of *Echiophis* however, appear to have been derived separately from a rather different *Ophichthus*-like ancestor (pop³ present, secondary cephalic pores absent, shorter snout, and spotted coloration). *Ophisurus porphyreus* Temminck and Schlegel, from Japan, tentatively placed in *Brachysomophis* by Kanazawa (1963), probably belongs in *Mystriophis*. *M. blastorhinos* Kanazawa, from French Guiana, is either an *Echiophis* or belongs in a separate genus. Kanazawa's illustration of the pore pattern of *M. blastorhinos* is somewhat inaccurate; pop³ and a single, rather than a double, interorbital pore are present (Kanazawa, in litt.).

Ophichthus Ahl

Ophichthus Ahl 1789: 5. Emended to *Ophichthys* by other authors. (Type species; *Muraena ophis* Linnaeus 1758, by original designation.)

Innominado Parra 1781: 96. A junior synonym of *Muraena ophis* Linnaeus 1758, non-binomial.

Ophis Turton 1807: 87. (Type species; "*O. maculata* . . . Spotted Serpent. Shaw Zool., iv. p. 22 . . . Bloch t. 154," presumably based on *Muraena ophis* Linnaeus 1758, by monotypy.)

Cogrus Rafinesque 1810a: 62. (Type species; *C. maculatus* Rafinesque 1810a, by monotypy.)

Ophithorax McClelland 1844: 212. (Type species; *Ophisurus ophis* Lacépède 1800, presumably based on *Muraena ophis* Linnaeus 1758, by Jordan, 1919b, as first reviser.)

Centrurophis Kaup 1856: 42 (2). (Type species; *Ophisurus spadiceus* Richardson 1844, as a misidentification of *Ophichthys cephalazona* Bleeker 1864, by Jordan, 1919b, as first reviser.)

Poecilocephalus Kaup 1856. 43 (5): (Type spe-

cies; *P. bonaparti* Kaup 1856, by monotypy.)

Microdonophis Kaup 1856: 43 (6). (Type species; *M. altipinnis* Kaup 1856, by monotypy.)

Coecilophis Kaup 1856: 44 (6) (Type species; *Ophisurus compar* Richardson 1844 = *Ophisurus apicalis* Bennett 1830, by monotypy.)

Herpetoichthys Kaup 1856: 44 (7). (Type species; *H. ornatissimus* Kaup 1856, by Jordan, 1919b, as first reviser.)

Muraenopsis LeSueur, *sic* Kaup 1856: 46 (11), *lapsus pro Muraenophis* Lacépède 1825.

Scytalophis Kaup 1856: 46 (13). (Type species; *S. magnioculis* Kaup 1856, by Jordan, 1919b, as first reviser.)

Leptorhinophis Kaup 1856: 46 (14). (Type species; *Ophisurus gomesi* Castelnau 1855, by Jordan, 1919b, as first reviser.)

Cryptopterus Kaup 1860: 11. (Type species; *C. puncticeps* Kaup 1860, by monotypy.)

Uranichthys Poey 1867: 256. (Type species; *Muraena hauannensis* Bloch and Schneider 1801 = *Muraena ophis* Linnaeus 1758, by Jordan and Davis, 1891, as first revisers.)

Oxydontichthys Poey 1880: 254. (Type species; *Ophichthys macrurus* Poey 1880 = *Ophisurus gomesi* Castelnau 1855, by original designation.)

Omochelys Fowler 1918: 3. Described as a subgenus of *Pisodonophis* Kaup. (Type species; *Pisodonophis cruentifer* Goode and Bean 1895, by original designation.)

Syletor Jordan 1919a: 343. (Type species; *Pisoodonophis cruentifer* Goode and Bean 1895, by original designation.)

Styletor Jordan 1919a, *sic* Jordan, Evermann, and Clark 1930: 86, *lapsus pro Syletor* Jordan 1919a.

Acanthenchelys Norman 1922: 296. (Type species; *A. spinicauda* Norman 1922, by original designation.)

Cryptopterenchelys Fowler 1925: 1. Described as a subgenus of *Ophichthus* Ahl. (Type species; *Cryptopterus puncticeps* Kaup, as a substitute name for *Cryptopterus* Kaup 1860, preoccupied.)

Zonophichthus Whitley 1930: 250. (Type species; *Ophichthys cephalazona* Bleeker 1864, by original designation.)

Gisenchelys Fowler 1944: 188. Described as a subgenus of *Ophichthus* Ahl. (Type species; *Ophichthys zophochir* Jordan and Gilbert 1881, by original designation.)

Syletophis Whitley 1950: 44. Substitute name for *Syletor* Jordan 1919a, preoccupied.

Antobrantia Ypiranga Pinto 1970: 13. (Type sp cies; *A. ribeiroi* Ypiranga Pinto 1970 = *Mu aena ophis* Linnaeus 1758, by original design tion.)

DESCRIPTION: Body moderately to very elongat laterally compressed posteriorly; body short than tail; snout moderately developed, subcon cal; lower jaw included; eye moderate to larg anterior nostril tubular, posterior along low edge of lip or opening into mouth; DFO abov or behind GO, but generally before pector tips; pectoral fin well developed; LL ossicles sep arated at pores; dentition variable, from num erous, small, and multiserial to few, large, an uniserial or biserial, never caniniform; teeth larg est at intermaxillary and on vomer and som times separated by a short gap; skull subtruncat posteriorly (fig. 2), orbit large; PO strut deve oped in some species (fig. 14); nasals and nas cartilage moderately developed; frontal and S crests moderately to well developed; maxill elongate, slender or rounded posteriorly (figs. 1 16); opercular series well developed, their ma gins entire (fig. 14); suspensorium nearly vertic to posteriorly inclined; otic bulla well deve oped; PG broad posteriorly, free and terete a teriorly; hyoid slender, HH separated from C by a narrow gap (fig. 17); branchiostegal ra slender, often numerous, unbranched and alon arch; UH a spike posteriorly; gill arches com plete, C_5 present, UP_3-UP_4 separate (fig. 18); pe toral girdle well developed, actinosts preser (fig. 19A); caudal vertebrae more numerous tha precaudal; coloration generally uniform, althoug banded or spotted species may be included.

ETYMOLOGY: From the Greek ὄφις (ophis), snake, and ἰχθύς (ichthus, mor correctly written ichthys; masculine), fish.

DISTRIBUTION: A circumtropical genus with ap proximately 55 species.

REMARKS: *Ophichthus* contains approximatel 55 valid species, for which no fewer than 2 nominal genera have been erected. The gener *Gisenchelys* Fowler and *Zonophichthus* Whitle are here included in the synonymy of *Ophich thus*. Hubbs' (1932) inclusion of *Ophis* Turto in the synonymy of *Ophichthus* was neither in cluded nor commented upon by Böhlke an Robins (1959) in their synonymy of *Ophichthu ophis*. Böhlke and Menezes (in litt.) have foun *Antobrantia*, type species *A. ribeiroi* Ypiran Pinto, to be an exact synonym of *Ophichth ophis*.

generic concepts of earlier authors, par-
y Kaup, are nearly all based on differ-
in coloration or dentition. I have at-
d to examine as many of these subgenera
sible. As broadly defined herein, *Ophich-*
xhibits a wide variety of morphological
ons, yet among the diverse types ex-
l, I have found no accompanying differ-
that are clearly generic. It is particularly
cing however, that the few osteological
ns within the genus that might merit gen-
cognition are present in *O. triserialis, O.*
:hir, and the type species, *O. ophis*. These
n the development of the postorbital strut
e posterior shortening of the maxilla.
ve attempted to identify subgeneric line-
ithin *Ophichthus*, using available generic
ms as subgeneric names. The following
s however, must be regarded as strictly
onal:

' ≅ tail; DFO above or before GO;
minute and uniserial throughout; col-
on of several species strongly spotted)....
.... subgenus *Microdonophis* Kaup

' shorter than tail; DFO behind GO,
rally above pectoral tips; teeth larger,
n multiserial ....

nterior nostril a broad tube, flared at
; intermaxillary block hooked down-
ard, and intermaxillary teeth directed
rizontally backward; tail tip hard and
arply-pointed; median fins conspicu-
usly expanded before tail tip ....
.... subgenus *Centrurophis* Kaup

nterior nostril tubular, not flared distally;
ntermaxillary teeth erect, with tips hook-
d back; tail tip hard and blunt, not
harply-pointed; median fins conspicu-
picuously expanded before tail tip ....
....................subgenus *Centrurophis* Kaup

Postorbital bones tightly sutured and bracing maxilla, forming a strut; maxilla rounded posteriorly; jaw and vomerine dentition bi- or triserial ....
.........................subgenus *Ophichthus* Ahl

Postorbital bones not tightly sutured and not forming a strut with maxilla; maxilla elongate and slender posteriorly; dentition variable, either uniserial or multiserial ....
.... subgenus *Coecilophis* Kaup

ded in the subgenus *Microdonophis* are:
ipinnis Kaup (IP), *M. erabo* Jordan and Snyder (IP), *Ophichthys polyophthalmus* Bleeker (IP)*, and *O. melanochir* Bleeker (IP).

Included in the subgenus *Centrurophis* are the generic types of *Zonophichthus* and probably *Poecilocephalus*. Included species: *Ophichthys cephalazona* Bleeker (IP), and *Poecilocephalus bonaparti* Kaup (IP)*.

Included in the subgenus *Ophichthus* are the generic types of *Innominado, Ophis, Cogrus, Uranichthys, Ophithorax,* and *Gisenchelys*. Included species: *Muraena ophis* Linnaeus (WA, EA), *Muraenopsis triserialis* Kaup (EP), and *Ophichthys zophochir* Jordan and Gilbert (EP). A complete synonymy of *O. ophis* is provided by Böhlke and Robins (1959).

Included in the subgenus *Coecilophis* is *Ophisurus apicalis* Bennett (IP), and presumably many other species listed below as *incertae sedis*.

Incertae sedis: Acanthenchelys spinicauda Regan (WA)*, *Cogrus maculatus* Rafinesque (M)*, *Conger urolophus* Schlegel (IP), *Cryptopterus puncticeps* Kaup (WA), *Echelus rufus* Rafinesque (M)*, *Omochelys marginatus* Fowler (WA) (= *Ophichthus cruentifer ?), Ophichthus asakusae* Jordan and Snyder (IP), *O. manilensis* Herre (IP)*, *O. melanoporus* Kanazawa (WA), *O. multiserialis* Norman (IP)*, *O. retifer* Fowler (IP)*, *O. roseus* Tanaka (IP)*, *O. stenopterus* Cope (IP)*, *Ophichthys ascensionis* Studer (WA)*, *O. ater* Peters (EP)*, *O. callensis* Günther (EP), *O. derbeyensis* Whitley (IP)*, *O. episcopus* Macleay (IP)*, *O. evermanni* Jordan and Snyder (IP), *O. frontalis* Garman (EP), *O. garretti* Günther (IP)*, *O. limkouensis* Chen (IP)*, *O. macrops* Günther (IP)*, *O. madagascariensis* Fourmanoir (IP)*, *O. melanochir* Bleeker (IP), *O. pacifici* Günther (EP), *O. retropinnis* Eigenmann (WA)*, *O. unicolor* Regan (IP)*, *O. woosuitingi* Chen (IP)*, *Ophisurus celebicus* Bleeker (IP)*, *O. gomesii* Castelnau (WA), *O. grandoculis* Cantor (IP)*, *O. macrochir* Bleeker (IP), *O. marginatus* Peters (IP)*, *O. parilis* Richardson (WA)*, *O. reguis* Richardson (EA)*, *O. remiger* Valenciennes (probably EP, no type locality given)*, *O. rutidoderma* Bleeker (emended by most authors to *rhytioderma*), (IP)*, *O. rutidodermatoides* Bleeker (emended by most authors to *rhytiodermatoides*), (IP), *Pisodonophis cruentifer* Goode and Bean (WA), *Scytalophis magnioculis* Kaup (WA)*, and two undescribed Eastern Pacific species.

Ophisurus Lacépède

Ophisurus Lacépède 1800: 195. (Type species; *Muraena serpens* Linnaeus 1758, as restricted

by Risso 1826.)

Leptognathus Swainson 1838: 334. (Type species; *L. oxyrhynchus* Swainson 1838 = *Muraena serpens* Linnaeus 1758, by original designation.)

Leptorhynchus Smith 1847: 244. (Type species; *L. capensis* Smith 1847 = *Muraena serpens* Linnaeus 1758.)

Anepistomon Gistel 1848: ix. A substitute name for *Leptorhynchus* Smith 1847, preoccupied.

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: body very elongate; snout attenuate, jaws elongate, slender, incapable of closing completely in adults; lower jaw included; anterior nostril lateral, at mid-snout (fig. 24B), posterior on outer lip and covered by a flap; DFO beyond tips of pectoral fins; cephalic surface sensory papillae well developed (figs. 24B, C); teeth conical, nearly uniserial, enlarged along vomer; maxilla elongate, slender and produced posteriorly; coloration uniform, darker dorsally.

ETYMOLOGY: From the Greek ὄφις (ophis), serpent, and οὐρά (oura), tail, and -ος (-us), masculine suffix.

DISTRIBUTION: Presumably a single species, known from the Mediterranean, eastern Atlantic, Cape of Good Hope, the western and central Indian Ocean, eastern Australia, New Zealand, and Japan. *Ophisurus macrorhynchus* Bleeker 1852, from Japan, differs slightly in morphometry from the Mediterranean *Muraena serpens*, yet a conclusive comparison has not been made.

REMARKS: The Atlantic and Pacific populations of *O. serpens*, if indeed conspecific, represent the most disjunct of known ophichthid distributions. Historically, the Mediterranean population could be explained as a relict of a Tethyan species. Parallels may be found in the disjunct populations of other eel species (see D. Smith, 1969), such as *Kaupichthys diodontus*, which presumably ranges from the western Atlantic, and the central and western Pacific, and Indian oceans (J. L. B. Smith, 1965), and *Dysomma anguillare*, presumably ranging from the tropical western Atlantic, Indian Ocean, and off Japan and China (Robins and Robins, 1970).

The identity of *Ophichthus multiserialis* Norman 1939 from the Gulf of Aden, included by J. L. B. Smith (1962: 455) in *Ophisurus*, has not been determined.

Oxystomus Rafinesque (1810b: 62) has been considered by most authors to be synonymous with *Ophisurus*. Castle (1969) however, has confirmed Bertin's (1935) suggestion that th species, *Oxystomus hyalinus*, is based on metamorphic *Serrivomer* rather than a *Ophisurus serpens*.

The external morphology and osteol *Ophisurus serpens* (as *O. novaezelandiae* H was described by Knox (1870).

Phyllophichthus Gosline

Phyllophichthus Gosline 1951a: 316. (Typ cies; *P. xenodontus* Gosline 1951a, by c designation.)

DESCRIPTION: Body moderately elongate, drical, laterally compressed posteriorly; b tail; snout produced, subconical, groov underside; lower jaw included; eye larg terior nostril subtubular, its posterior bord tending downward into leaflike appendage terior nostril opens into mouth; GO v crescentic, shorter than isthmus; dorsal ar fins low, expanded before the sharply p tail tip; DFO above GO; pectoral fin w veloped; pop^3 absent; LL canal ossicles ar coils separated at pores; teeth conical, r and uniserial in jaws, recurved on mandib sent from vomer; neurocranium elongat truncate posteriorly, orbit large; PO strut nasals and nasal cartilage well developed absent; maxilla fragile and not produced, lated ca. mid-vomer (fig. 16); preoper duced; suspensorium anteriorly incline angle ca. 100°; otic bulla moderately deve PG slender, short, and pointed anteriorly; slender, HH absent, CH with a minute a condyle (possibly a remnant of a fused branchiostegal rays numerous, filamentou from hyoid; UH split anteriorly, produce teriorly as a slender spike; gill arches pharyngeal teeth minute, C_3 absent, H_1 only at tip; pectoral girdle well develope nosts present; precaudal vertebrae more erous than caudal; coloration uniform.

ETYMOLOGY: From the Greek φυλλο lon), leaf, and *Ophichthus* (masculine), a of ophichthids, in reference to the leaf-li terior nostrils.

DISTRIBUTION: Two described Pacific s *P. xenodontus* Gosline from the central an ern Pacific and Indian oceans, and *P. m* McKay*, described from Australia.

Pisodonophis Kaup

Pisodonophis Kaup 1856a: 47. Also spe

›phis by other authors. (Type species; *›urus cancrivorus* Richardson 1844, as :ted by Bleeker 1865.)

›nophis Kaup 1856b: 17. *Emend. pro onophis* Kaup 1856a.

heirophis Fowler 1944: 190. (Type spe- *Pisodonophis daspilotus* Gilbert, in Jor- and Evermann 1898, by original designa-

PTION: General characteristics those of *thus*. Differences include: pectoral fin ›ased; pop^3 present or absent; teeth mol- or granular, multiserial on jaws and vo- rgest at intermaxillary with a short gap ing those of the vomerine block; PO strut maxilla elongate, slender posteriorly; ›st branchiostegal rays free from hyoid; f pharyngeal plates generally small, pave- ‹e; pectoral girdle reduced, actinosts ab- : absent in one species; coloration gen- niform, spotted in one species.

LOGY: From the Greek πίσος pea, ὀδους (odons), tooth, and ις (ophis; masculine), serpent.

ɪUTION: Known from 8-10 species, a ropical genus. Included are: *Ophisurus* ›*rus* Richardson (IP), *O. boro* Hamilton- an (IP), *O. hijala* Hamilton-Buchanan). *hoevenii* Bleeker (IP), *O. hypselopterus* (IP)*, *O. semicinctus* Richardson (EA)*, *›ophis copelandi* Herre (IP), *P. daspilotus* (EP), *Pisoodonophis zophistus* Jordan and (IP) (=*P. cancrivorus?*), *Ophichthys dro-* ;ünther (EA)*.

KS: The relationships of *Pisodonophis*, *'hys*, and their *Ophichthus*-like ancestors :ussed in the remarks on *Myrichthys*.

chelys Fowler, considered by recent au- o be a junior synonym of *Pisodonophis*, referred to *Ophichthus*. *Omochelys cru-* is unlike the species of *Pisodonophis* in few branchiostegal rays, all of which are d to the hyoid.

;uly and Nag (1964) described the func- norphology of the pectoral girdle and the l myomeric musculature of a fish they ed as *Ophichthus boro*. The pectoral hey have crudely illustrated is clearly not *Pisodonophis boro*, and is probably from es of *Ophichthus*. Tilak and Kanji (1967) their error and properly described the ›logy of the pectoral girdle of *Pisodono-phis boro* in relation to its habit.

Pogonophis Myers and Wade

Pogonophis Myers and Wade 1941: 78. (Type species; *P. fossatus* Myers and Wade 1941, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout blunt; jaws subequal, a single pendulous barbel on upper lip; eye large; anterior nostril tubular, with a posterior tag; DFO behind GO; pectoral fin minute; tail tip pointed; preopercular pores vertically, not obliquely aligned, pop^3 absent; LL ossicles nearly continuous; teeth pointed, uniserial except on maxillae where biserial, largest at intermaxillary which is continuous with those of vomer; skull subtruncate posteriorly, orbit large; PO strut absent; nasals and nasal cartilage reduced; SOC weakly pointed; maxilla elongate, slender posteriorly; suspensorium posteriorly inclined, jaw angle ca. 80°; otic bulla moderately developed; PG broad posteriorly, free and terete anteriorly; hyoid slender; HH separated from CH by a broad gap; branchiostegal rays numerous, all slender and associated with hyoid, the anteriormost 3-4 rays fused basally; UH broad anteriorly, short and slender posteriorly; gill arches reduced, C_5 absent, UP_3-UP_4 separate; pectoral girdle weakly developed, actinosts absent; caudal $\cong$ precaudal vertebrae; coloration strongly spotted.

ETYMOLOGY: From the Greek πωγων (pogon), beard, and ὄφις (ophis; masculine), serpent, in reference to the consipcuous barbel on the snout.

DISTRIBUTION: A single eastern Pacific species, ranging from the Gulf of California to Peru (as *Ophichthus afuerae* Hildebrand).

Quassiremus Jordan and Davis

Quassiremus Jordan and Davis 1891: 622. (Type species; *Ophichthus evionthas* Jordan and Bollman 1889, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout developed, conical, a short groove on underside; lower jaw included; eye large; DFO behind GO; pectoral fin minute; tail tip pointed; pop^3 present; LL ossicles continuous; teeth pointed, uniserial, largest at intermaxillary and continuous with those

of vomer; skull truncate posteriorly, orbit large; PO strut absent; nasals well developed, nasal cartilage weakly developed; SOC strongly pointed; maxilla elongate, slender posteriorly; opercular margins entire; suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG broad posteriorly, free and terete anteriorly; hyoid slender, HH separated from CH by a broad gap: branchiostegal rays numerous, all slender and associated with hyoid, the anteriormost 3-4 rays fused basally; UH broad anteriorly, short and slender posteriorly; gill arches reduced, C_5 absent, UP_3-UP_4 separate; pectoral girdle reduced to a slender Cl and SCl; caudal = precaudal vertebrae; coloration strongly spotted.

ETYMOLOGY: From the Latin *quassus*, obliterated, and *ramus* (masculine), oar, in reference to the minute pectoral fins.

DISTRIBUTION: Known from 3 New World species. Included are: *Ophichthus evionthas* Jordan and Bollman (EP), *Ophichthys nothochir* Gilbert (EP) (including *Q. parvipinna* Seale), and *Quassiremus productus* Seale (WA) (including *Q. goslingi* Beebe and Tee-Van).

REMARKS: The osteological description of *Quassiremus* is based on *Q. nothochir*. *Q. evionthas*, the generic type, was examined from radiographs and gill arch dissection.

Scytalichthys Jordan and Davis

Scytalichthys Jordan and Davis 1891: 635. Described as a subgenus of *Mystriophis* Kaup. (Type species; *Ophichthys miurus* Jordan and Gilbert 1882, by original designation.)

DESCRIPTION: Body cylindrical, moderately elongate, longer than tail; snout very short, flat, subconical; jaws elongate, lower jaw inferior; eye moderate; anterior nostril in a short tube, posterior opens into mouth; GO low lateral, crescentic, longer than isthmus; DFO well behind pectoral tips; pectoral fin reduced; tail tip bare, sharply pointed; pop^3 absent; LL ossicles continuous, not separated at pores; teeth strong, conical, those on maxilla in two widely separated rows, uniserial on dentary; those on vomer large, uniserial, widely separated, and continuous with those on intermaxillary; skull subtruncate posteriorly, orbit reduced; PO not bracing maxilla; nasals very reduced, nasal cartilage reduced; SOC absent, a short broad posterior projection; maxilla elongate, bifurcate posteriorly, the distal section elongate and terete, the medial and pointed; opercular series well de their margins entire; suspensorium near cal, hyomandibular strongly ridged; otic b developed; PG slender, a fine point an hyoid arch slender, HH widely separat CH; branchiostegal rays numerous, all unbranched, and along arch; UH a sho posteriorly; C_5 short, UP_3-UP_4 nearly fuse pharyngeal plate elongate; pectoral gi duced, SCl and actinosts absent; IM bon and CTP well developed; caudal vertebr than precaudal; coloration strongly spot

ETYMOLOGY: From the Greek σκυ· (skytale), viper, and ιχθυς (ichth culine), fish.

DISTRIBUTION: A single eastern Pacific ranging from the Galapagos Islands to of California and Guadalupe Island.

REMARKS: Schultz (1942) has commer the generic status of *Scytalichthys* with r it dentition.

Xyrias Jordan and Snyder

Xyrias Jordan and Snyder 1901: 864. (Ty cies; *X. revulsus* Jordan and Snyder 1 original designation.)

DESCRIPTION: Body cylindrical, mo elongate, longer than tail; snout short, cal; jaws elongate, the lower inferior; e erate; anterior nostril non-tubular, laterall with a minute ventral flap; posterior no side mouth and covered with a flap; GO eral, crescentic, longer than isthmus; D hind pectoral tips; pectoral fin moder tip bare, pointed; pop^3 absent; teeth conical, not extremely enlarged; those c largest, uniserial, and nearly continuo those of intermaxillary, jaw teeth mu orbit depressed; PO not bracing maxilla and nasal cartilage reduced; SOC with posterior projection; maxilla elongate, l posteriorly; opercular series well de their margins entire; suspensorium near cal; PG slender, tapering to a fine p teriorly; hyoid arch moderately slender, arated from CH by a gap; branchiosteg erous, slender, unbranched and along ossified, UP_3-UP_4 united by a suture; girdle complete, SCl, Cl, Sc, Co, and visible in radiograph; IM bones, ribs, well developed; caudal vertebrae fewer t caudal; coloration of numerous small sp

LOGY: From the Greek ξυρίας ine), a shaveling, in reference to the ab- f cirri on the lips.

3UTION: A single species from Japan. (1973) reported that it is caught occasion- shrimp trawlers in the Misaki, Kochi, and ɔ prefectures.

KS: This description was prepared from aphs and a gill arch dissection of the e.

'ison with Previous Classifications

results of the present study offer certain into the reliability of superficial morpho- characters as a basis for classification. The :cent attempt at a compilation of genera the Ophichthidae was that of Rosenblatt :Cosker (1970). That study was based on ysis of previous literature and an exami- of all recognized genera except *Neen-* *Malvoliophis*, and *Benthenchelys* (Castle, 'as the first to suggest that *Benthenchelys* ɔhichthid). The following discrepancies ex- veen the results of that study and the :

:helus was included in the Myrophinae elinae), following Gosline (1952); in the study *Echelus* is shown to be an ophich- and the presence of a caudal fin is not d as a definitive character separating the hid subfamilies;

eptenchelys was included in the Myro- again based on the caudal condition; in :sent study it is suggested that its rela- ɔs lie with the Bascanichthyini;

imnostoma was considered to be syn- us with *Caecula;* in the present study gical characters have been identified that s generic separation;

Dmochelys was considered to be synony- with *Pisodonophis* on the basis of tooth ers; in the present study it is indicated affinities lie closer to species of *Ophich-* ıan of *Pisodonophis*, and *Omochelys* is 'ely placed in the synonymy of *Ophich-* vaiting a revision of that large and cum- e genus;

:nkinsiella, and *Microdonophis* and *Zono-* *'us*, were recognized at the generic level; present study no osteological characters :en found to support their generic recog- and they are reduced to subgeneric rank *Cirrhimuraena* and *Ophichthus*, respec- tively.

The results of this comparison however, have shown that the previous classification, based for the most part on external morphological characters, was not seriously upset by a classification based primarily on osteology. The finding of greatest consequence was that the affinities of *Echelus* lie with the Ophichthinae rather than the Myrophinae; the caudal fin condition was shown to be trivial when compared with the "*Ophichthus*-like" condition of numerous osteological characters.

In that the majority of classification schemes within the teleosts are now based on external morphological characters, it is somewhat reassuring to realize that at least within the Ophichthidae, the external morphological classification parallels that based on osteology.

EVOLUTION OF THE OPHICHTHIDAE

Relationship to other Anguilliforms

Recent authors have summarily recognized 23 families within the suborder Anguilloidei (Greenwood, et al., 1966; Gosline, 1971). Subsequent studies have changed this listing in the following manner. Robins and Robins (1970) have expanded the Dysommidae to include the Dysomminidae and the Nettodaridae and (1971) provisionally united the Nessorhamphidae with the Derichthyidae. Smith (1971) has provisionally removed *Coloconger* from the Congridae and erected the family Colocongridae. The abovementioned authors have allocated the anguilloid families to five superfamilies, namely: the Anguilloidea (those eel families with paired frontals), Synaphobranchoidea (Synaphobranchidae, Dysommidae and Simenchelyidae), Congroidea (Congridae, Colocongridae, Muraenesocidae, Nettastomidae, and Macrocephenchelyidae), Nemichthyoidea, and Ophichthoidea.

The superfamiliy Ophichthoidea is restricted to the Ophichthidae. They appear most closely related to the superfamily Congroidea, but differ in the condition of several major characters (several fundamental characteristics of the Ophichthidae and related apodal families are indicated in Table 7). As Smith (1971) has shown, the congroids possess a complete pterygoid arch and a nearly complete gill arch skeleton. Conversely, the ophichthid pterygoid is reduced and well separated from the vomer, and their gill arches exhibit various stages of reduction. The ophichthids also differ from the congrids in possessing

numerous and overlapping branchiostegal rays, a fused frontal commissure, and a cartilaginous connection between the first epibranchial and second infrapharyngobranchial of the gill arch skeleton. Certain congrids, primarily within the subfamily Heterocongrinae, are similar to ophichthids in the development of laminar ribs, reduced neural spines, an elongate body, and a fleshy tail tip (cf. Böhlke, 1957; Rosenblatt, 1967). Rosenblatt discussed these similarities and suggested (p. 95) that "the superficial similarties between *Gorgasia* and the ophichthids are certainly parallel adaptations to a similar mode of life, and the minor osteological similarities may be adaptations as well."

The general condition of the primitive ophichthid genera, viz., *Echelus* and *Ophichthus*, appears to be derived from a congrid ancestor. To my knowledge, no known congrid exhibits definitive ophichthid characters in an intermediate state of development, particularly the fused frontal commissure and overlapping branchiostegal rays. The achievement of the ophichthid condition may have been a quantum jump in apodal evolution, attained by either an advanced congrid or congrid ancestor by means of a rapid integration of the above mentioned characters. Yet this may only be presumed until further evidence from extant or fossilized species is obtained.

Evolution within the Ophichthidae

The purposes of any classification sys to best reflect the phylogenetic history taxa involved and to provide predictabili that a newly discovered taxon might be placed without upsetting the system. Ar tionary scheme may only be inferred fro ing data, and must carefully weigh th abilities related to each hypothetical p In dealing with supra-specific categories, faced with the difficulty of delineating on a subjective basis. The history of the thidae, however, would suggest that the tribe, and subfamily reflect certain bi realities in an evolutionary sense. The study has attempted to define and identi groupings. The presence of several fund ostelogical characters in both major line Ophichthidae suggests a monophyletic c the family. These characters include the commissure, the epibranchial intercon and the unique manner of branchiosteg lap. The two subfamilies differ trenchant manner in which the branchiostegal ray tached to the hyoid, yet this difference preclude a monophyletic origin. The subfamilial and tribal evolution within t ichthidae is illustrated below in Figure eric evolution within each tribe is treat following discussion.

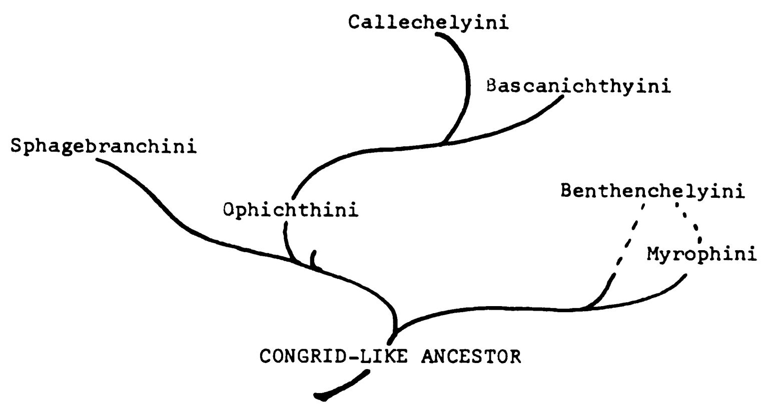


Figure 37. Proposed evolutionary relationship of ophichthid tribes.

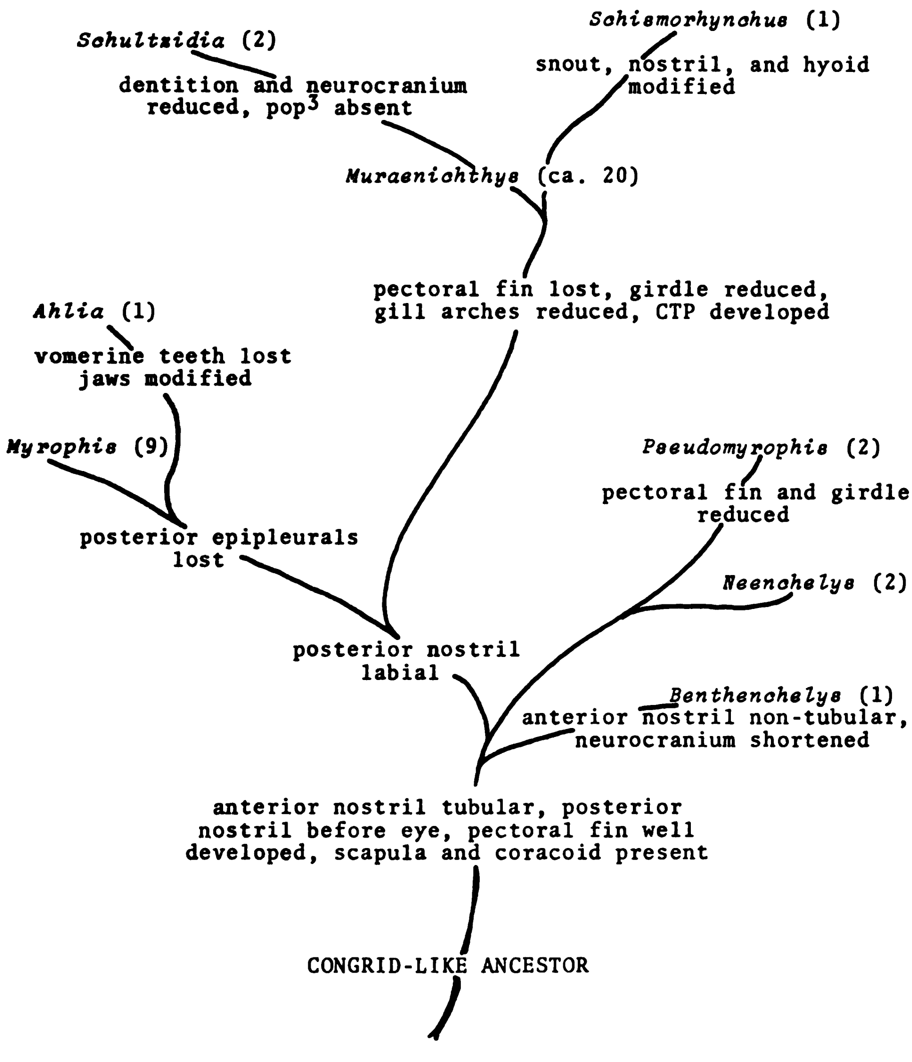


Figure 38. Proposed evolution of the Myrophinae. Number of species in parentheses.

Myrophini and Benthenchelyini. Two conditions indicate that the Myrophinae probably arose from the first dichotomy of the ophichthid lineage (Figs. 37-38). These are the presence of a well developed caudal fin and the unique myrophine branchiostegal condition in which the majority of the rays are free from and well behind the epihyal. The attached rays, like those of the congirds, are basally broadened. Although the species of *Echelus* possess a myrophine-like caudal fin, they also possess an ophichthine-like hyoid and other osteological conditions that link them with the Ophichthinae.

Primitive conditions of certain characters within the Myrophinae include:

(a) teeth present on the dentary, intermaxillary, maxilla, and vomer;
(b) pectoral fin moderately to well developed;
(c) coracoid and scapula present;
(d) posterior nostril lateral;
(e) first basibranchial ossified;
(f) seven attached branchiostegals along epihyal;
(g) anterior nostril tubular;
(h) eye not enlarged, its diameter ten or more in head length.

Benthenchelys cartieri, the single species within the Benthenchelyini, is highly specialized for its unique adaptation to a pelagic existence (see Remarks on *Benthenchelys*). It has however, retained certain primitive conditions which would suggest that it separated early from the ancestral myrophine stock. *Benthenchelys* possess all the primitive conditions listed above except that its first basibranchial has been reduced to cartilage. Whether *Benthenchelys* separated before, after, or along with the *Neenchelys-Pseudomyrophis* lineage was not discerned from the available data. The posterior nostril of *Neenchelys* and *Pseudomyrophis*, like that of *Benthenchelys*, is lateral. The nostril of *Benthenchelys* is extremely atypical within the Ophichthidae in that it is markedly more dorsally located than it is in other genera. The partial re-ossification of the third hypobranchial in *Benthenchelys* probably represents a secondary specialization; the third hypobranchial of all congrids, and presumably that of the basal ophichthids, is cartilaginous.

Similarities between *Neenchelys* and *Pseudomyrophis* were described earlier in this study. These genera have retained the first basibranchial, the pectoral fin, and pectoral girdle, but an attached branchiostegal has been lost in two of the three species examined. *Pseudomyrop* become specialized in the reduction of i toral fin and girdle, and in one species th has become extremely elongate. *Neench* somewhat more primitive in that it has re a developed pectoral fin and its girdle reduced.

Beyond the level of the *Pseudomyrophis-chelys* separation, the posterior nostril h come labial in position. In general, the o thid posterior nostril lies within the mo along the lip and is covered by a flap. The sion to the more generalized and presu primitive condition in which the posterior lies along the outer edge of the lip has achieved numerous times. This is eviden the contrasting posterior nostril conditic closely related genera such as *Ichthyapu Apterichtus, Ophichthus* and *Ophisurus*, an ticularly between the species of *Muraeni* A distinction however, should be made be the condition of the earlier-removed myr genera *(Benthenchelys, Pseudomyrophis, Neenchelys)* and that of the remaining o thids. In no case does it appear that the po nostril has secondarily returned to a congr placement.

The next major dichotomy is that of the *Myrophis* lineage. That they arose from a mon ancestor is evidenced by their consp specialization in which the pleural ribs ar ited to the anterior trunk vertebrae. The s of *Myrophis* differ considerably in extern pearance, primarily in body and snout e tion, even though they differ little osteolo *Ahlia egmontis*, by comparison, is speciali having lost the vomerine dentition, post shortened maxillae, modified pterygoid hypohyals either lost or fused to the cera and the dorsal fin origin withdrawn to th of the anus.

The remainder of the Myrophini compri species of *Muraenichthys, Schultzidia, Schismorhynchus*, commonly called the eels". The reductions and specializations latter two genera must preclude them as tors to *Muraenichthys* or to each other. *Muraenichthys* however, are species suffi generalized that either *Schismorhynch Schultzidia* might have been derived from As discussed in the remarks on *Muraeni* subgeneric lineages, although including divergent extremes, are bridged by a broa trum of morphological conditions. The mo

›ecies of the subgenus *Scolecenchelys* ancestors to the subgenus *Muraenich-* the genera *Schultzidia* and *Schismor-* ›pecies of *Scolecenchelys* have the pos- tril within the mouth, separate upper l tooth plates, an ungrooved snout, r biserial conical teeth, and a third pre- pore (pop^3). Species of the subgenus *thys* have an external posterior nostril, granular dentition, a deep body, a ıt, and fused upper pharyngeal teeth. ›s of *Schultzidia* have lost the pop^3 and ion is extremely reduced, being absent mer, absent or embedded on the inter- and minute or villiform in the jaws. *ynchus labialis* is specialized in quite : manner, and seems to have been de- m a *Muraenichthys*-lineage different of *Schultzidia*. It is an elongate worm ıs undergone specializations apparently ı its mode of feeding. A prominent ›oove divides the underside of the snout ıds anteriorly to the elongate tubular he suspensorium is forwardly inclined, ugh the dentition is generalized, the aryngeal tooth plates are fused, and l arch members (H_3 and I_3) are absent.

:hini. The Ophichthini include the most and generalized of ophichthids. Primi- tions of certain characters include:

lal rays developed;
:oral, dorsal, and anal fins well devel-

chiostegal rays fewer than 20;
h conical, often multiserial, present on ›ntary, vomer, and intermaxillary;
ı ceratobranchial (C_4) ossified as a d, upper pharyngeal tooth plates sepa-

preopercular pore (pop^3) present;
›ocranium truncate posteriorly;
approximately 60 percent of the total

cies of *Echelus* possess all of the above and represent one branch of the oph- ineage (Fig. 39). All subsequent oph- re specialized in having the tail tip re- a finless point. Although differences he condition of the tail tip, in no in- e caudal rays developed as in *Echelus* nyrophines. The genus *Ophichthus*, as defined herein, is the most generalized remaining ophichthine genera, having character states that embrace most of the varia- tion of the other genera. The changes in other genera have to do with the loss or specialization of characters, or rearrangements of the basic *Ophichthus* condition. Certain lineages within *Ophichthus* appear ancestral to lineages within the tribe itself. For example, those species with few branchiostegal rays and an average body taper probably gave rise to the long-jawed pi- scivorous genera. The proposed sphagebranchin lineage can also be derived from generalized ophichthin characters.

Ophisurus appears to be an offshoot from a moderately elongate *Ophichthus*-like species with few branchiostegals, nearly uniform denti- tion, and well developed surface sensory papil- lae. Its jaws and neurocranium modifications merit its generic recognition.

The species of *Quassiremus* share several prim- itive characters with *Ophichthus*, but have be- come specialized through the reduction of the pectoral fin and loss of the C_4 and pectoral girdle elements.

The species of *Pisodonophis, Myrichthys*, and *Cirrhimuraena* probably arose from a common lineage, evidenced in their increased number of branchiostegals and generally multiserial denti- tion. *Cirrhimuraena* is specialized in the devel- opment of labial cirri. Differences between the species of *Cirrhimuraena* are probably deserving of subgeneric rank, as discussed in the remarks on this genus. *Pisodonophis* and *Myrichthys* share several unique simlarities, primarily their multiserial molariform dentition and broad-based pectoral fins. *Myrichthys* is further specialized in the loss of pop^3, the reduction of the pectoral fin and girdle, and the advancement of the DFO. As mentioned in the remarks on *Myrichthys*, a nearly continuous character series exists from species of *Ophichthus* → *Pisodonophis* → *Myrichthys*.

The species of *Mystriophis, Echiophis, Brachy- somophis, Aplatophis, Xyrias*, and *Scytalichthys* form a natural group of predaceous ophichthines specialized for the capture of large struggling prey. These specializations include the develop- ment of a postorbital strut to brace the maxilla, the strengthening of the suspensorium, enlarge- ment of the vomerine and jaw dentition, the ad- vancement and dorsal location of the eyes on the snout, and the attainment of a large size as adults. Certain species of Ophichthus *(O. ophis, O. triserialis*, and *O. zophochir)* are similarly specialized. The character states of *Echiophis*

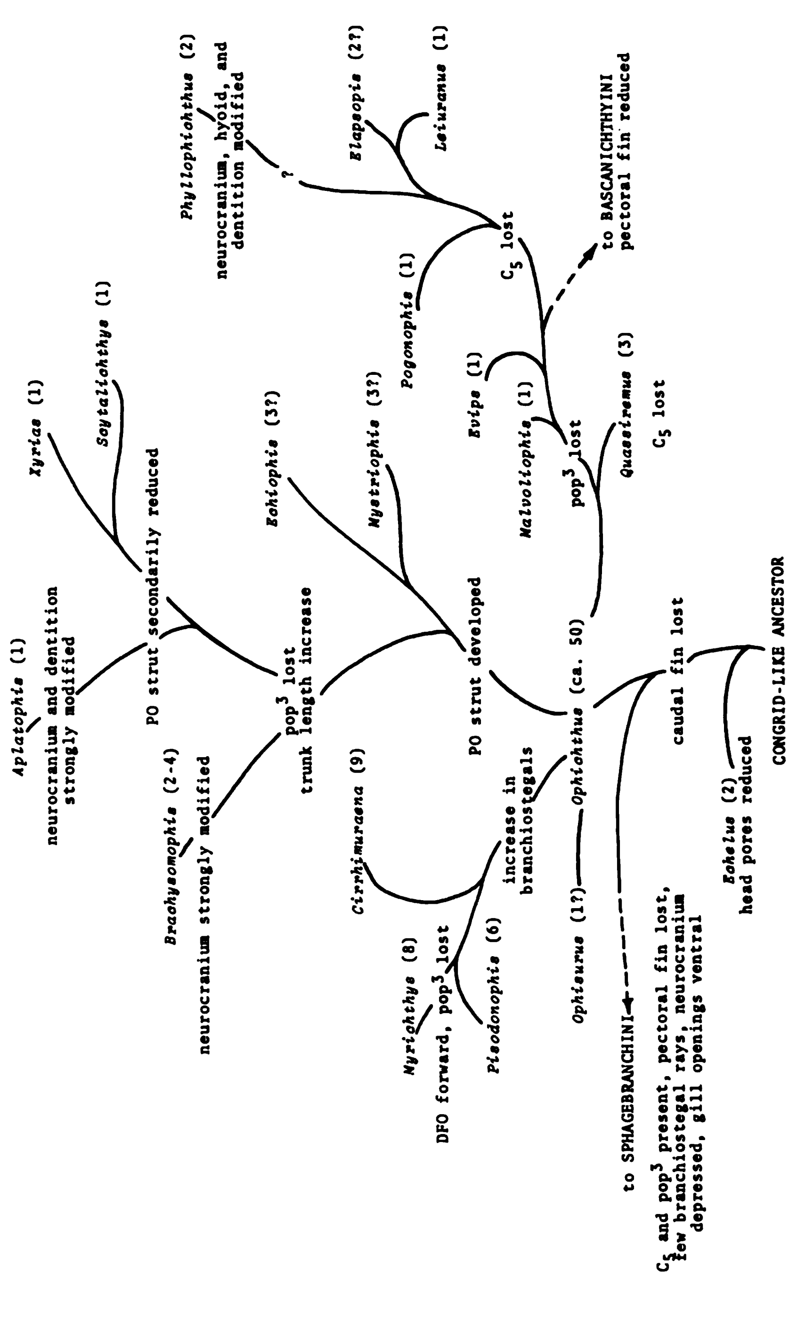


Figure 39. Proposed evolution of the Ophichthini.

lystriophis are merely further specializa-)f the condition of those species of *Oph-* s. As mentioned in the remarks on *Mystri-* the specializations of *E. blastorhinos*, when · investigated, may merit generic recogni- :emaining genera in the lineage are further lized by having a proportionately longer region, or conversely, a shorter tail, and lost the pop[3]. The examined species of *'somophis* have developed labial cirri and sive postorbital strut. The translocation of bit to the snout tip and development of ırface sensory papillae system in *Brachy-* ı*his* and *Scytalichthys* correlate with the g behavior; these species, like those of ı*his* (personal observation, and Hiatt and ırg, 1960), lie within their burrows with ıeir snout tips exposed, awaiting the pas- ıf prey items. The advantages of the eye ın and papillae development are obvious. lar feeding behavior is practiced by other ıthines. Species of *Callechelys*, for ex- have been observed (personal observa- nd R. H. Rosenblatt, personal communica- with the head protruding from the sand ı, apparently awaiting the passage of prey *Callechelys* has not undergone the devel- ıt of the strengthened suspensorium and ted jaws and associated orbit translocation of the long-jawed ophichthines, and feeds ily on relatively smaller and weaker prey. evelopment of labial cirri in *Brachysomo-* ınd other ophichthine genera probably as a screen to prevent fine sediment from ıg the mouth. The absence of the post- strut in the remaining genera is assumed a secondary reduction. *Xyrias* and *Scytal-* ; are quite similar in the shape of their ıe and in the condition of their multiserial on. *Scytalichthys* has a proportionately trunk region and has a further modified condition. *Aplatophis* is conditionally at the apex of this lineage. Its numerous ions and specializations make its place- vithin the lineage difficult.

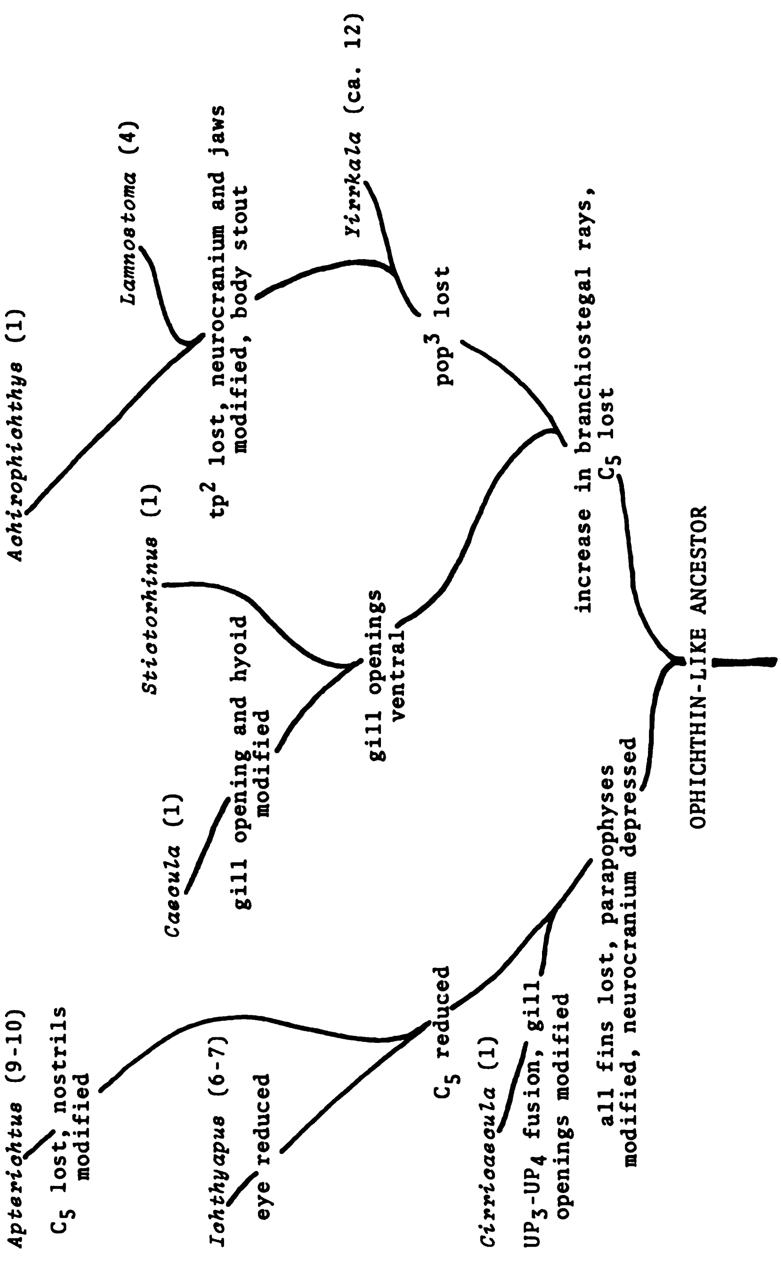
remaining ophichthine genera have lost)p[3]. *Malvoliophis* has diverged from the ıthus condition in having an advanced :*vips* has retained an *Ophichthus*-like DFO, s a considerably reduced pectoral fin and and a proportionately reduced tail length. cestral bascanichthyin probably arose from eage, and probably possessed an anterior ın ossified C_5, and a reduced pectoral fin and girdle. Subsequent ophichthins have lost the rod-like ossified C_5 possessed by all other ophichthins. *Pogonophis*, although similar in external appearance to species of *Ophichthus*, is specialized in its development of labial barbels and by its loss of the C_5 and pop[3]. *Leiuranus* and *Elapsopis* are closely-related genera which have departed from *Ophichthus* in snout shape, UP_3-UP_4 fusion, and reduced pectoral fins and girdles; *Leiuranus* is further specialized in the loss of vomerine dentition and certain pectoral elements. *Phyllophichthus* is aligned with this lineage although its exact placement is undetermined. Its suspensorium, jaws, dentition, and neurocranium are extremely modified.

Sphagebranchini. The Sphagebranchini comprise a specialized ophichthin offshoot of highly modified species, assembled on the basis of the absence of the pectoral fin, pectoral girdle reductions, and low or entirely ventral gill openings. Primtive conditions of certain characters include:

(a) neurocranium depressed;
(b) branchiostegal rays fewer than 20;
(c) pop[3] and tp[3] pores present;
(d) C_5 ossified;
(e) dorsal and anal fins present;
(f) anterior nostrils tubular, posterior nostrils within mouth;
(g) body and tail nearly subequal;
(h) gill openings low lateral.

The interpretation of intergeneric relationships within this tribe is made difficult by the reduction or loss of numerous characters. Several interpretations are possible, depending upon the importance applied to certain characters. The following interpretation, in assuming the tribe to have had a monophyletic origin, assumes that the C_5 has been lost independently in two lineages. This loss seems plausible through an ossified → cartilaginous transformation, and has apparently occurred elsewhere in the family.

The preliminary dichotomy separates the three sharp-snouted, entirely finless genera (Fig. 40). Each possesses a peculiar projection from the parapophyses of the anterior trunk vertebrae (Fig. 33A), a specialization not observed elsewhere in the tribe. *Cirricaecula* is primitive in having retained an *Ophichthus*-like C_5 but specialized in its UP_3-UP_4 fusion, entirely ventral non-converging gill openings, and labial cirri development. The species of *Ichthyapus* have a small eye, reduced anterior nostril, and cartilaginous C_5. Species of *Apterichtus* have entirely lost


Achirophichthys (1)
Lamnostoma (4)
Yirrkala (ca. 12)
tp^2 lost, neurocranium and jaws modified, body stout
pop^3 lost
Stictorhinus (1)
gill opening and hyoid modified
gill openings ventral
increase in branchiostegal rays, C_5 lost
Caecula (1)
OPHICHTHIN-LIKE ANCESTOR
Apterichtus (9-10)
C_5 lost, nostrils modified
Ichthyapus (6-7)
eye reduced
C_5 reduced
Cirricaecula (1)
UP_3-UP_4 fusion, gill openings modified
all fins lost, parapophyses modified, neurocranium depressed

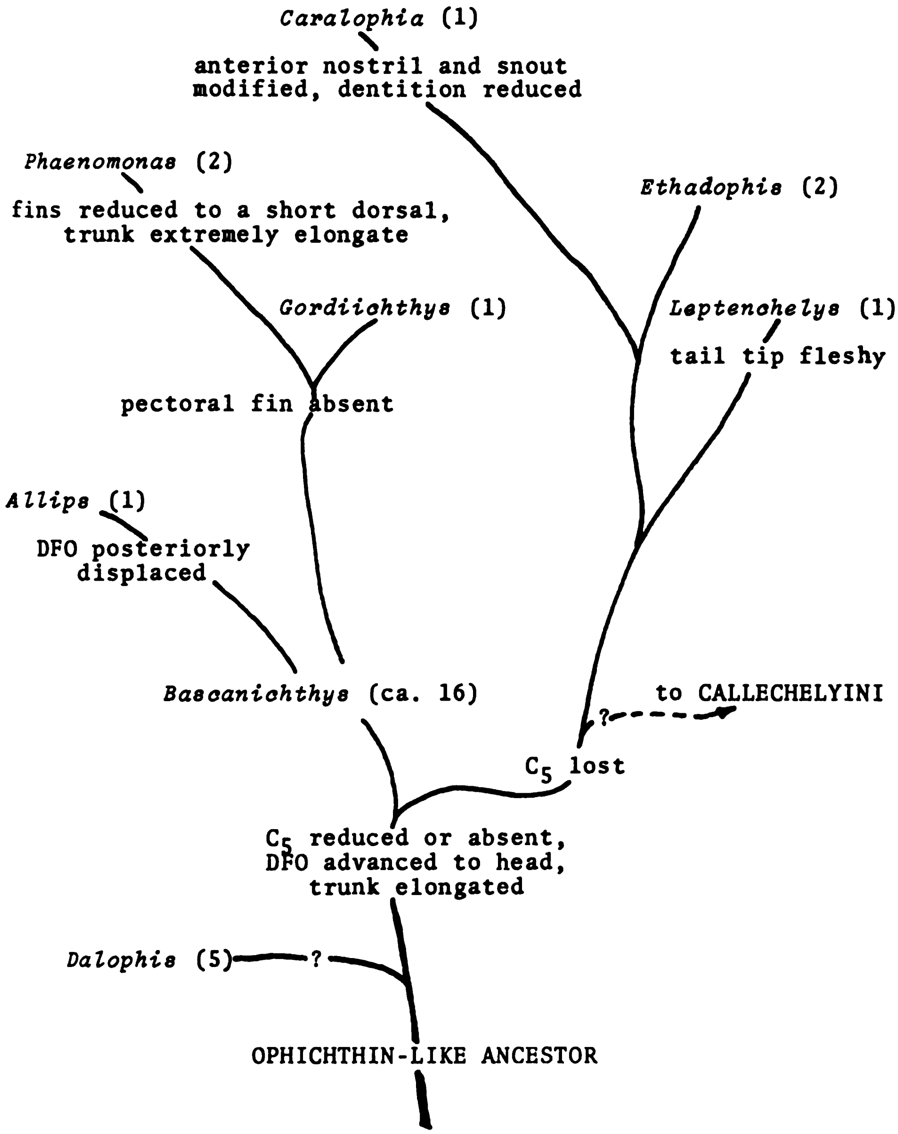


Figure 41. Proposed evolution of the Bascanichthyini.

the C_5 and the posterior nostril is translocated to the outer lip.

The remaining genera are characterized by an increased number of branchiostegals and the loss of the C_5. They may be separated into two major lineages. *Caecula* and *Stictorhinus* are similar to the finless sphagebranchins in having ventral gill openings, pointed snouts, and moderately depressed neurocrania; these similarities, in part, may be adaptations to a similar mode of life. The derivation of *Yirrkala* and the closely-related *Achirophichthys* and *Lamnostoma* is somewhat uncertain. They have lost the pop[3] and have low lateral to ventral gill openings. The neurocrania of these genera are considerably modified from the broad, depressed state of other sphagebranchins. The neurocranium of *Yirrkala* is rounded dorsally. That of *Lamnostoma* has become narrowed along the ethmoid, in probable correlation with its enlarged dentition and related to its feeding mode. Certain species of *Yirrkala* have retained the tp[2]. The species of *Yirrkala* are generally elongate whereas those of *Achirophichthys* and *Lamnostoma* are cylindrical and stout.

Bascanichthyini. The Bascanichthyini, like the Sphagebranchini, appear to be derived from a moderately specialized ophichthin-like ancestor. Certain specializations in the form of hyoid modifications and fin reductions had already been achieved by their supposed ophichthin-like ancestor. As adults, the bascanichthyins have specialized toward a burrowing, vermiform existence, feeding on small prey and rarely leaving the substrate. As noted in the discussion of the axial skeleton (p. 45), the trunk elongation of species of *Phaenomonas, Allips,* certain *Bascanichthys* and presumably *Gordiichthys* is a specialization for this mode of life. Primitive conditions of certain characters within the Bascanichthyini include:

(a) pectoral fin rudimentary;
(b) eye small, but not minute;
(c) C_5 present, but reduced;
(d) body and tail nearly subequal;
(e) branchiostegal rays numerous;
(f) DFO behind head;
(g) snout grooved on underside;
(h) gill openings low lateral in position.

The inclusion of *Dalophis* in the Bascanichthyini is uncertain. Although possessing *Ophichthus*-like body/tail proportions and an ossified C_5, it appears more similar to the bascanichthyin condition in its fin reductions and general cephalic appearance. As a bascanichthy placed near the primary separation f ancestral lineage (Fig. 41).

The remaining genera appear to be from the generalized conditon of *Basca* The rudimentary pectoral fin is retained *Allips*. *Allips* is similar to species of *B. thys* in its trunk elongation and gener ognomy, but differs in its presumably s ily-derived posterior DFO. *Phaenomona* ther specialized through reduction from age and has become nearly finless. *Gor* not examined in this study, is provisic ferred to this lineage on the basis of c included in its terse description. The r bascanichthyins are somewhat similar general morphologies, and have under eral modifications and reductions from *canichthys* condition. The Callechelyini in assumed to be derived from a bascar like ancestor, but have further special radiated along a different complex of characters.

Callechelyini. The Callechelyini is distinct and compact of ophichthine tr species are among the most specialize ichthids and are quite removed from t tral ophichthid stock. Their specializa reductions impart a particular facies to that readily separates it from other op particularly evidenced in the ventral, c gill openings, laterally compressed bc tail, anterior dorsal fin origin, small reduced pore systems. These outer s are borne out by the shortened neur stout hyoid, and the osteological red the pectoral apparatus and gill arch further characterize the group.

These conditions appear to have rived from a bascanichthyin-like ancest an ophichthin ancestor which gave ri Bascanichthyini. Available specimens graphs of 20 of the 22 species of the (ini have allowed an in-depth study of The meristic and morphological charac in Tables 8-9 were used to generate puter-programmed taxonomic evaluat trated in Figures 43-44. The charact computer programs WVGM and REG described in the taxonomic methods s this study.

Primitive conditions of certain key within the Callechelyini include:

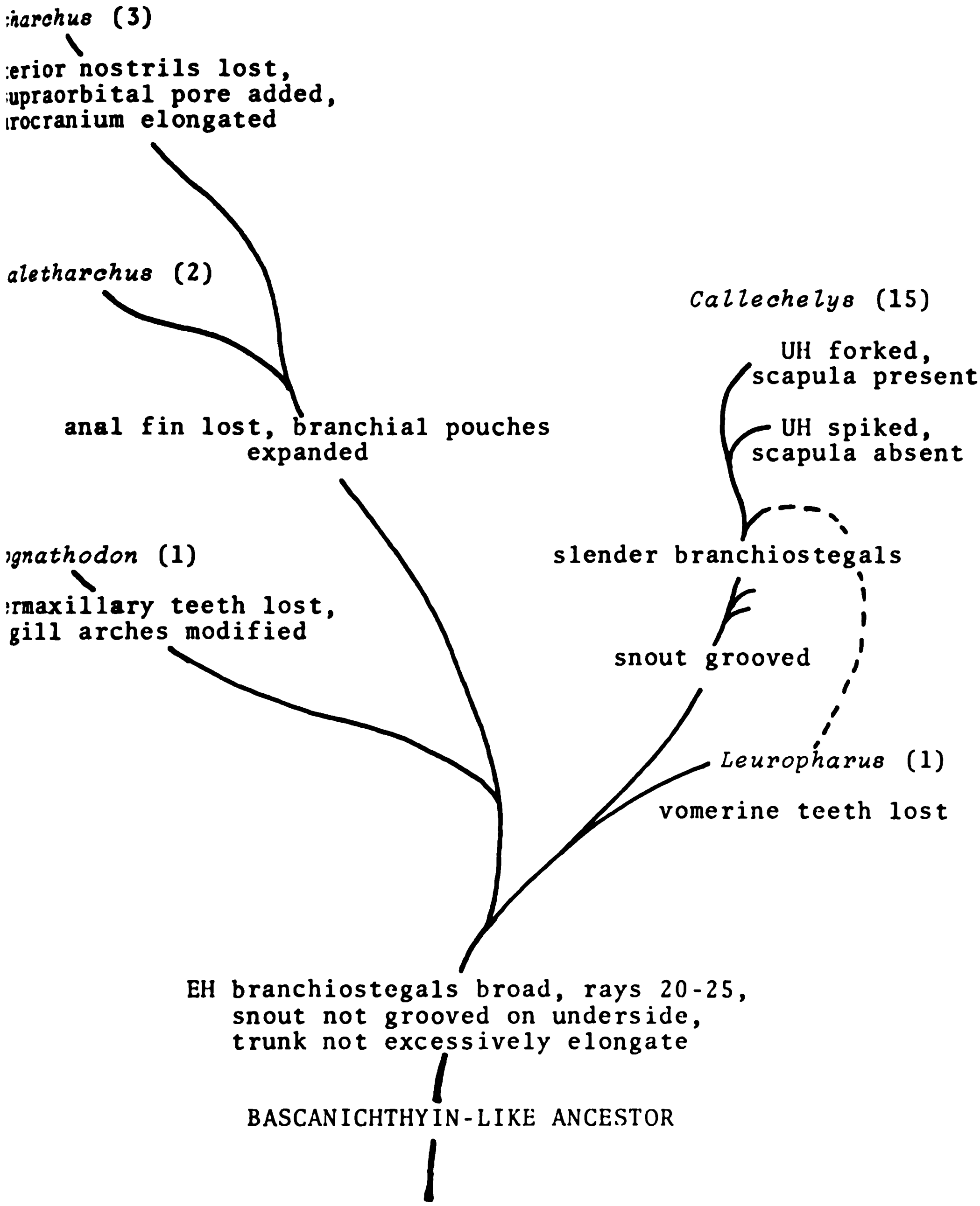


Figure 42. Proposed evolution of the Callechelyini.

(a) teeth uniserial and present on the dentary, intermaxillary, maxilla, and vomer;

(b) underside of snout not grooved;

(c) gill openings low and bascanichthyin-like, not specialized as in *Letharchus* and *Paraletharchus;*

(d) branchiostegal rays fewer than 25 pairs, those along the epihyal broadened basally;

(e) three supraorbital pores;

(f) trunk not extremely elongate, tail 40 percent or more of total length;

(g) urohyal ossified and spike-like, not forked posteriorly;

(h) two longitudinal rod-like pectoral elements.

No living tribal member possesses all the primitive characters listed above. However *Aprognathodon platyventris* and certain species of *Callechelys,* except for minor specializations, closely approximate the above conditions.

The retention of several primitive characters suggests that *Aprognathodon platyventris* separated early from the basal stock (Fig. 42). It has become specialized through the loss of intermaxillary dentition and the incomplete re-ossification of the third hypobranchial. These conditions are probably adaptations to a specialized mode of feeding.

The next dichotomy in the tribal evolution involved two other New World genera, *Letharchus* and *Paraletharchus* (compare Figs. 42-44). They, like *Aprognathodon,* have retained the broad branchiostegals and ungrooved snouts, but are specialized in having broadly flared branchial pouches and in the loss of the anal fin. Species of *Paraletharchus* appear externally quite similar to species of *Callechelys;* species of *Letharchus* are quite distinctive in having lost the tubular anterior nostril condition, added a fourth supraorbital pore, and having more elongate and depressed neurocrania.

The remaining callechelyins include *Leuropharus lasiops* and the numerous species of *Callechelys. Leuropharus* is somewhat generalized in having few vertebrae, a moderate tail length, and an ungrooved snout, yet it differs from other callechelyins in lacking teeth on the vomer. Whether it separated before the species of *Callechelys* or from a *Callechelys*-like ancestor is questionable in that *L. lasiops* appears to have numerous, slender branchiostegals (observed from a radiograph of the type specimen). This condition, if observed correctly, is more advanced than that of certain species of *Callechelys (C. nebulosus, C. springeri,* and *C. holochromus),* and would necessitate the evolution of this condition if *Leurophar*ι rated earlier than *Callechelys.*

The remaining genus, *Callechelys* with ognized species, has apparently combiı generalized callechelyin condition with minor specializations into a very successfυ plan". Evolution within *Callechelys,* as d on page 63, has included two or thrє separations from the ancestral stock, whi followed by two major subgeneric lines. *elys nebulosus, C. springeri,* and perhaps *chromus* have retained broadened branch rays, which is probably correlated to the erate number. These two conditions are ɼ responsible for the separation of these from other *Callechelys* species in p WVGM and REGROUP (Figs. 43-44). Thє ditions should not preclude their inclusioı *Callechelys* and illustrates the weakne numerical taxonomic scheme based on characters. The remaining species are ized in having more numerous and branchiostegal rays, and a longer trunk and an increase in the number of trunl brae. These species have evolved along tı ages, one containing species which have a simple urohyal and lost the posterior girdle element (the scapula?), and anotł species in which the urohyal is split po into two slender divergent rays but with ond pectoral element retained. Neither specializations, when compared with t other ophichthids, seems to merit gener ration.

Zoogeography and Comments on Ophicht Speciation

In the absence of a suitable fossil recc virtually impossible to reconstruct with the past distribution and center of origiı Ophichthidae. Certain inferences relatinį cestral distributions however, can be mad on the present species distribution, assuı vironmental tolerances of ophichthids in and the presumed geological history of land and water masses.

Two major geological events have diı fected the distribution of tropical marinє isms. These were the Miocene (?) closurı Tethyan Seaway through the convergencı European and African continental plates and Forsyth, 1972), isolating the Meditı and Atlantic from the Indo-Pacific, and

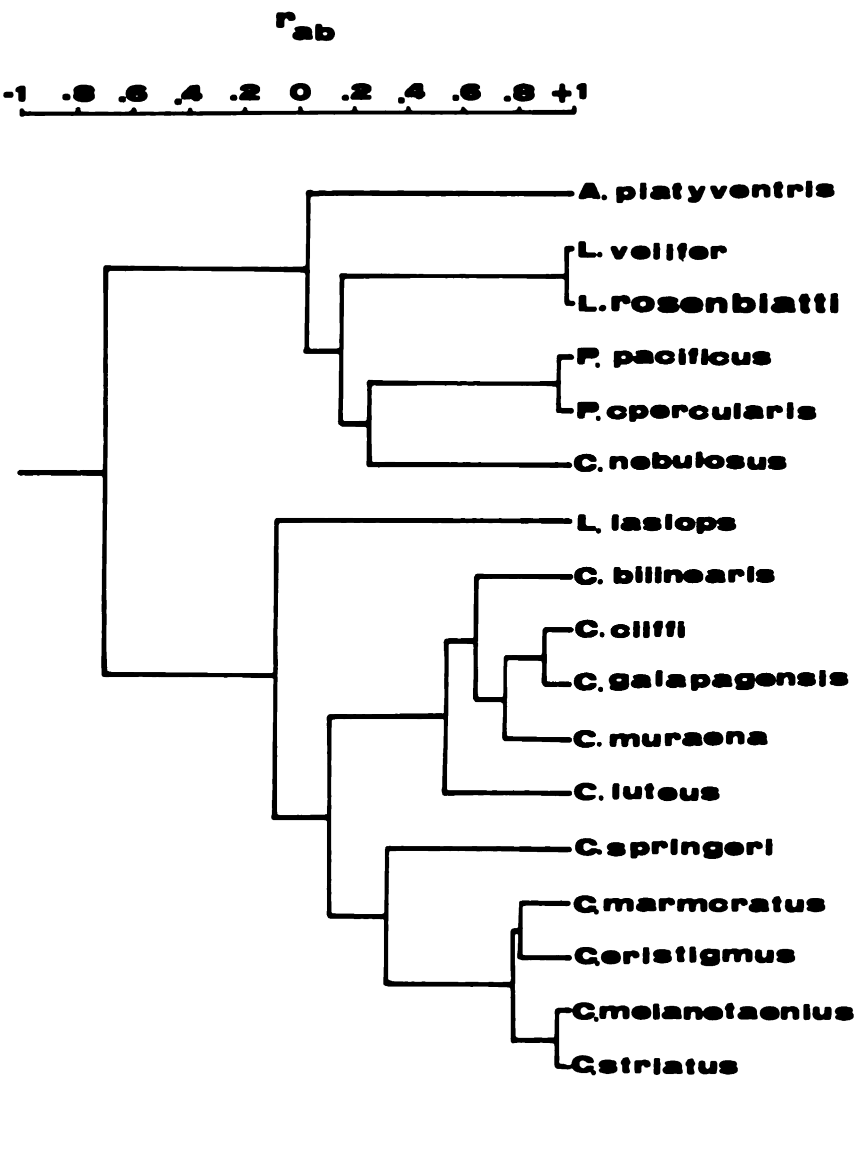


Figure 43. Phenogram of the relationships of the species of the Callechelyini, using program WVGM. The levels of correlation at which species join are represented by the scale r_{ab}.

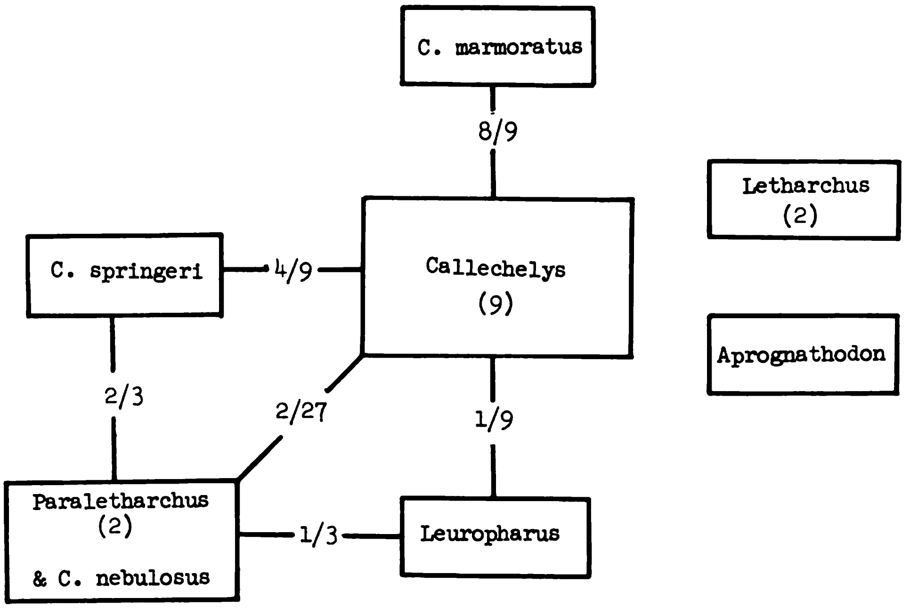


Figure 44. Interrelationships of species groups of the tribe Callechelyini, as defined by program REGROUP. Significance level set at 0.600. Fractions are the ratios of the number of observed between-group species connections to the maximum number of possible connections. Number of species represented per genus are within parentheses. Not included are *Callechelys bitaeniatus, C. holochromus, C. leucopterus,* and *Letharchus aliculatus.*

Pliocene to Pleistocene closure (Whitmore and Stewart, 1965) of the Middle American Seaway, separating the New World oceans (Rosenblatt, 1963). Assuming that the environmental tolerances of the Ophichthidae have always limited them to tropical, sub-tropical, or warm temperate waters, it may be stated that the Tethyan and Central American Seaway closures have delimited, in large part, the waters available to the distribution of living genera. (A single exception may be the distribution of *Ophisurus serpens* in the Mediterranean, and eastern and western African shores, probably resulting from a transgression of the Cape of Good Hope.) Applying these assumptions to the known distribution of ophichthid genera (Table 10), inferences concerning the evolution and generic interrelationships of the family may be drawn. For example, the seven circumtropical genera must have existed prior to the closure of the Tethyan Seaway, or have passed through the Central American Seaway and transgressed both oceans. Recent inf tion gained from investigations of plate tec and paleomagnetism suggests that the A Ocean during the Early Cretaceous was narrower than at present (Phillips and Fc 1972). On that basis, the distribution of chaic species across the Tethyan Seaway an the eastern Pacific would seem quite plausbl

An *Ophichthus*-like genus probably exis the Upper Eocene, as evidenced by S (1896) description of *Eomyrus dolloi* fro Wemmelian Formation of western Europ neurocranium, as illustrated, is much like a modern *Ophichthus.* Those genera res to both coasts of the New World (Tab Group III) must have existed prior to the manian uplift, and now include several p closely related species. *Echiophis* is also a ber of this group but has presumably ext its distribution to the eastern Atlantic. The *Muraenichthys* is presently limited to th

dian Ocean, western and central Pacific with a single south eastern Pacific spe- own only from the offshore Chilean is- of Juan Fernandez and San Felix. Its ab- rom the tropical Atlantic, as explained by cer (1970), perhaps suggests a post-Teth- igin of the genus rather than the lack in antic of a suitable habitat. The single New species is probably recently derived from ith-western Pacific by means of eastward rt across the South Pacific. The restriction ny genera to the Indo-Pacific and New oceans (Table 10, Groups II, IV-V) prob- presents radiations since the Tethyan and I American Seaway closures, respectively. rigin of genera with species distributed major water masses might be inferred in analysis of the species involved. The *Phaenomonas*, for example, contains an Pacific species (*P. pinnata*) which ranges he Gulf of California to Colombia, and an acific species (*P. cooperae*) which ranges lawaii to east Africa. The extreme speciali- of *P. cooperae*, in comparison to *P. pin-* night suggest that *Phaenomonas* arose in stern Pacific and radiated westward. Its ied absence from the Atlantic Ocean indicate that *Phaenomonas* either evolved he bascanichthyin stock since the closure Central American Seaway, or that proper *monas* habitat is presently unavailable in lantic. Another explanation might assume ie present existence of the primitive *P.* in the eastern Pacific is the result of tward radiation from an Indo-Pacific ori- llowed by further specialization of the an- stock through competition with the more x ophichthid fauna of the Indo-Pacific. 1 however, must be applied in any of the assumptions concerning the present dis- n of ophichthid genera. Modern collect- thods have resulted in the discovery of ous new species, many of which repre- new genera, and it is highly likely that extant ophichthid species remain uncol-

analysis of the distribution of species ophichthid genera reveals several inter- biological phenomena. The classification ed here is hopefully more than just a con- cataloguing system, and assumes that proportionate number of species in vari- hichthid genera, ranging from a single in nearly half of the genera to more than 50 in *Ophichthus*, reflects something real in the natural system. Figure 45 illustrates the distribution of species among the genera of the Ophichthidae, Gobiesocidae, and the blenniid tribe Salariini. These examples were chosen because they represent recent monographic revisions, uncomplicated by the efforts of a multiplicity of authors; the gobiesocid data are from Briggs (1955) and subsequent species descriptions and the blenny data are based on Smith-Vaniz and Springer (1971). A pattern exists in the three groups illustrated, and if transformed to logs, the data would indicate an almost straight-line inverse relation between the log-number of species/genus and the log number of genera. C. B. Williams (1964) has discussed similar evidence from a number of terrestrial groups and suggested that such a log-normal mathematical pattern is a recurrent phenomenon in natural systems. He observed that the fit of these data to a calculated log series is moderately good at most levels, but higher than expected for monotypic genera.

The following hypotheses are proposed to explain the distribution of species among genera. One hypothesis might assume that such a distribution of species among genera reflects the evolution of a group with many recently-derived genera, and a decreasing number of genera which have existed for increasingly longer time spans. Those archaic genera have had the opportunity through geologic time and events to segregate and speciate, whereas the more recent taxa have lacked those opportunities. A more intriguing hypothesis however, suggested by Richard H. Rosenblatt (personal communication), might assume that a combination of characters exist in the ancestral lineage from which taxa radiate by means of specializations and reductions; certain resultant taxa would include a combination of characters which would allow further radiation (dependent upon certain biological factors and geological events) resulting in genera with numerous species, whereas other taxa have specialized in a manner which, in relation to the available environments, has a low probability of further radiation. The latter category contains the numerous monotypic genera of the Ophichthidae. These monotypic genera might represent evolutionary "forays" into rather unique environments or life styles and are apparently unsuccessful beyond their present limited area of distribution or as ancestral bases for further speciation. The former category, in which

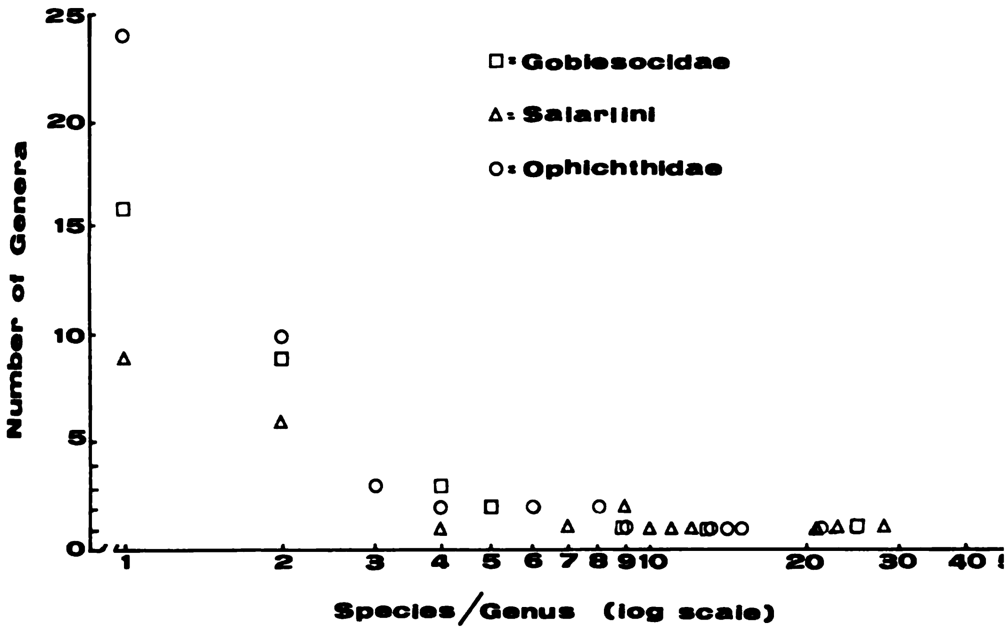


Figure 45. Distribution of species among the genera of the Ophichthidae, Gobiesc cidae and Salariini.

few genera contain many species, contains such genera as *Myrichthys, Callechelys,* and *Ophichthus,* in which the combination of adaptive characters selected for have, with minor modifications, resulted in the numerous species which occupy similar habitats in all tropical oceans. Biological factors such as the leptocephalus larval stage and geological events such as seaway closures lend credence to the first mentioned hypothesis and complicate the second. present distribution and few species of presumably archaic ophichthid genera tend to support the latter hypothesis.

Further investigations into the ecolo behavior of species of this intriguing and eel family may offer further insight into t lutionary processes which have shap Ophichthidae.

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Table 1. Dentition of the Genera of Ophichthidae

Abbreviations are: +, present; -, absent. Shape: C, conical; F, fang-like M, molariform; V, villiform. Rows in jaws and vomer: B, biserial; M, multi serial; U, uniserial. I-V signifies intermaxillary-vomerine.

	Shape	Rows in Jaws	Vomer	I-V G.
Benthenchelyini				
Benthenchelys	C	U	U	+
Myrophini				
Ahlia	C	U	-	-
Muraenichthys	C,M	U,B,M	U,B	-
Myrophis	C	U,B	U,B	-
Neenchelys	C	U	B	-
Pseudomyrophis	C	U	U	-
Schismorhynchus	C	U	U	-
Schultzidia	V	U	-	
Callechelyini				
Aprognathodon[1]	C	U	U	-
Callechelys	C	U	U,B	+
Letharchus	C	U	U	+
Leuropharus	C	U	-	
Paraletharchus	C	U	U	+
Sphagebranchini				
Achirophichthys	C,F	B	U	?
Apterichtus	C	U	U	+
Caecula	C	U	U	+
Cirricaecula	C	U	U	+
Hemerorhinus	?	?	?	?
Ichthyapus	C	U	U	+
Lamnostoma	C,F	U,B	U	+
Stictorhinus	C	U	U	+
Yirrkala	C	U	U	+
Bascanichthyini				
Allips	C	U	U	
Bascanichthys	C	U	U	
Caralophia	C	U	U	
Dalophis	C	U	U	
Ethadophis	C	U	U	
Gordiichthys	C	U	U	
Leptenchelys	C	U	U	
Phaenomonas	C	U	U	
Ophichthini				
Aplatophis	F	B	U	
Brachysomophis	C,F	U[2]	U	
Cirrhimuraena	C	U,B	U,B	
Elapsopis	C	U	U	
Echelus	C,V	M	M	
Echiophis	C	B	B	
Evips	C	U[2]	U	
Leiuranus	C	U	-	
Malvoliophis	C	U	U	
Myrichthys	M	B,M	M	
Mystriophis	C,F	U	U	
Ophichthus	C	U,B,M	U,B	
Ophisurus	C,F	U	U	
Phyllophichthus	C	U	-	
Pisodonophis	M	B,M	B,M	
Pogonophis	C	U[2]	U	
Quassiremus	C	U	U	
Scytalichthys	C,F	U[2]	U	
Xyrias	C	M	U	

1. Intermaxillary teeth absent
2. Maxillary teeth biserial, dentary uniserial

Table 2. Number and Location of Branchiostegal Rays of the Species of the Ophichthidae

Counts represent the right side only. Rays joined basally are counted separately. "CH-EH" represents the cartilaginous CH-EH interspace. "Free" rays are noticeab y separated from the hyoid.

	Tota	Free	Along CH	CH-EH	Along EH
Benthenchelys cartieri	20	13	-	-	7
Ahlia egmontis	47	41	-	-	6
Muraenichthys chilensis	32	25	-	-	7
Muraenichthys gymnopterus	43	36	-	-	7
Muraenichthys macropterus	31	37	-	-	4
Myrophis plumbeus	43	37	-	-	6
Myrophis uropterus	32	26	-	-	6
Myrophis vafer	49	42	-	-	7
Neenchelys buitendijki[1]	30	24	-	-	6
Pseudomyrophis micropinna	47	40	-	-	7
Pseudomyrophis nimius	23	17	-	-	6
Schismorhynchus labialis	30	25	-	-	5
Schultzidia johnstonensis	33	29	-	-	4
Aprognathodon platyventris	28	-	14	2	12
Callechelys bilinearis	27	-	21	1	5
Callechelys eristigmus	31	-	5	6	20
Callechelys galapagensis	27	-	15	2	10
Callechelys marmoratus	29	-	18	2	9
Callechelys melanotaenius	29	-	12	3	14
Callechelys nebulosus	29	10	8	3	8
Letharchus rosenblatti	34	-	16	3	15
Paraletharchus pacificus	32	-	23	4	5
Apterichtus flavicaudus	16	1	1	1	13
Caecula pterygera	25	12	-	3	10
Cirricaecula johnsoni	18	-	1	3	14
Ichthyapus selachops	19	-	4	2	13
Lamnostoma orientalis	29	26	-	-	3
Stictorhinus potamius	29	-	5	4	20
Yirrkala lumbricoides	27	-	5	2	20
Yirrkala misolensis	29	-	12	2	15
Yirrkala tenuis	25	-	4	3	18
Bascanichthys panamensis	30	1	5	3	21
Caralophia loxochila	27	-	8	4	15
Phaenomonas cooperae	28	19	3	5	1
Phaenomonas pinnata	26	19	1	6	-
Aplatophis chauliodus	22	-	2	1	19
Brachysomophis sauropsis	17	-	2	1	14
Cirrhimuraena macgregori	24	-	7	2	15
Cirrhimuraena taeniopterus	29	6	1	4	18
Echelus myrus	15	-	4	-	11
Echelus pachyrhynchus	18	-	4	1	13
Echiophis sp.	21	-	4	1	16
Elapsopis cyclorhinus	24	4	2	1	17
Leiuranus semicinctus	31	-	6	3	22
Malvoliophis pinguis	21	-	4	1	16
Myrichthys colubrinus	30	-	22	3	5
Myrichthys maculosus	35	-	9	2	24
Myrichthys xystrurus	31	3	3	1	24
Ophichthus cephalozona	27	2	2	2	21
Ophichthus cruentifer	17	-	4	-	13
Ophichthus frontalis	19	-	5	1	13
Ophichthus triserialis	22	-	3	-	19
Ophichthus zophochir	27	-	5	1	21
Ophisurus serpens	19	-	2	1	16
Phyllophichthus xenodontus	29	22	-	-	7
Pisodonophis boro	31	1	6	2	22
Pisodonophis cancrivorus	30	6	1	1	22
Pisodonophis daspilotus	32	8	-	3	21
Quassiremus nothochir	21	2	2	-	18
Scytalichthys miurus	25	-	4	2	19

1. From Nelson (1966a: fig. 2a)

Table 3. Gill Arch Condition in the Ophichthinae

Abbreviations are: B_{1-4}, basibranchials; H_{1-3}, hypobranchials; C_{1-5}, ceratobranchials; I_{2-3}, infrapharyngobranchials; UP_{3-4}, upper pharyngeal dermal tooth plates; 0, ossified; -0-, UP_3-UP_4 fusion; C, cartilaginous; R, rudimentary; -, absent; *, from Nelson (1966a: Table 1).

	B_1	B_2	B_3	B_4	H_1	H_2	H_3	C_{1-4}	C_5	I_2	I_3	UP_3	UP_4
Ophichthus zophochir	0	C	R	C	0	0	C	0	0	0	0	0	0
O. rhytidodermatoides	0	C	-	-	0	0	C	0	0	0	0	0	0
*O. polyophthalmus**	0	C	R	R	0	0	C	0	0	0	0	0	0
O. altipinnis	0	-	-	-	0	0	C	0	0	0	0	0	0
O. erabo	0	C	C	R	0	0	C	0	0	0	0	0	0
O. cruentifer	0	-	-	-	0	0	C	0	0	0	0	0	0
O. cephalazona	0	R	-	-	0	0	C	0	0	0	0	0	0
Pisodonophis boro	0	-	R	R	0	0	C	0	0	0	0	0	0
P. cancrivorus	0	R	C	C	0	0	C	0	0	0	0	0	0
Ophisurus serpens	0	C	C	C	0	0	C	0	0	0	0	0	0
Evips percinctus	0	C	R	R	0	0	C	0	0	0	0	0	0
Echelus myrus	0	C	C	C	0	0	C	0	0	0	0	0	0
E. pachyrhynchus	0	C	-	C	0	0	C	0	0	0	0	0	0
Myrichthys colubrinus	0	C	-	-	0	0	C	0	0	0	0	0	0
M. maculosus	0	C	-	C	0	0	C	0	0	0	0	0	0
M. xystrurus	0	C	-	C	0	0	C	0	0	0	0	0	0
Aplatophis chauliodus	0	-	-	-	0	0	C	0	0	0	0	0	0
Brachysomophis sauropsis	0	C	-	C	0	0	C	0	0	0	0	0	0
*B. henshawi**	0	C	-	C	0	0	C	0	0	0	0	0	0
Cirrhimuraena macgregori	0	C	R	R	0	0	C	0	0	0	0	0	0
C taeniopterus	0	-	R	-	0	0	C	0	0	0	0	0	0
*Echiophis intertinctus**	0	R	R	C	0	0	C	0	0	0	0	0	0
Echiophis sp.	0	C	C	C	0	0	C	0	0	0	0	-0-	
Xyrias revulsus	0	C	-	C	0	0	C	0	0	0	0	-0-	
Malvoliophis pinguis	0	C	R	R	0	0	C	0	0	0	0	-0-	
Elapsopis cyclorhinus	0	C	R	-	0	0	0	0	-	0	0	-0-	
Leiuranus semicinctus	0	C	-	C	0	0	C	0	-	0	0	-0-	
Phyllophichthus xenodontus	0	C	R	-	0	0	C	0	-	0	0	0	0
Pogonophis fossatus	0	C	-	-	0	0	C	0	-	0	0	0	0
Quassiremus evionthas	0	-	-	-	0	0	C	0	-	0	0	0	0
Q. nothochir	0	-	-	-	0	0	C	0	-	0	0	0	0
Dalophis imberbis	0	C	C	R	0	0	0	0	0	0	0	0	0
*Bascanichthys teres**	0	C	-	C	0	0	C	0	0	0	0	0	0
B. panamensis	0	-	-	C	0	0	C	0	-	0	0	0	0
Allips concolor	0	C	-	C	0	0	C	0	-	0	0	0	0
Ethadophis byrnei	0	C	-	-	0	0	C	0	-	0	0	0	0
E. merenda	0	C	R	C	0	0	C	0	-	0	0	0	0
Phaenomonas pinnata	0	C	-	C	0	0	C	0	-	0	0	0	0
Caralophia loxochila	0	-	C	C	0	0	C	0	-	0	0	-0-	
Callechelys marmoratus	0	C	-	-	0	0	C	0	-	0	0	0	0
Aprognathodon platyventris	0	C	-	-	0	0	0	0	-	0	0	0	0
Paraletharchus pacificus	0	C	-	R	0	0	C	0	-	0	0	0	0
*Letharchus velifer**	0	C	-	R	0	0	C	0	-	0	0	0	0
Letharchus rosenblatti	0	C	-	R	0	0	C	0	-	0	0	0	0
Ichthyapus selachops	0	-	-	C	0	0	C	0	0	0	0	0	0
Cirricaecula johnsoni	0	-	-	R	0	0	C	0	0	0	0	-0-	
Apterichtus flavicaudus	0	-	-	-	0	0	C	0	-	0	0	0	0
Caecula pterygera	0	C	C	C	0	0	C	0	-	0	0	0	0
Yirrkala lumbricoides	0	C	C	C	0	0	C	0	-	0	0	0	0
Y. tenuis	0	R	C	C	0	0	C	0	-	0	0	0	0
Y. misolensis	0	C	C	C	0	0	C	0	-	0	0	0	0
Y. kaupi	0	C	C	C	0	0	C	0	-	0	0	0	0
Lamnostoma orientalis	0	C	-	-	0	0	C	0	-	0	0	0	0
Stictorhinus potamius	0	C	C	C	0	0	C	0	-	0	0	0	0

Table 4. Gill Arch Condition in the Myrophinae

Abbreviations as in Table 3.

	B_1	B_2	B_3	B_4	H_1	H_2	H_3	C_{1-4}	C_5	I_2	I_3	UP_3	UP_4
Benthenchelys cartieri	C	-	-	-	0	0	0	0	-	0	0	-0-	
Ahlia egmontis	0	-	-	-	0	0	-	0	-	-	0	0	0
*Myrophis punctatus**	0	R	-	-	0	0	C	0	-	0	0	0	0
M. vafer	0	-	-	-	0	0	C	0	-	0	0	0	0
M. uropterus	0	-	-	-	0	0	C	0	-	0	0	0	0
M. plumbeus	0	-	-	-	0	0	C	0	-	0	0	-0-	
Pseudomyrophis nimius	0	-	-	-	0	0	C	0	-	0	0	0	0
P. micropinna	0	C	-	-	0	0	C	0	-	0	0	0	0
*Neenchelys buitendijki**	R	-	-	-	0	0	C	0	-	0	0	0	0
Schultzidia johnstonensis	-	-	-	-	0	0	C	0	-	-	0	-0-	
Schismorhynchus labialis	-	-	-	-	0	0	-	0	-	-	0	-0-	
Muraenichthys chilensis	-	-	-	-	0	0	C	0	-	0	0	0	0
M. macropterus	-	-	-	-	0	0	C	0	-	C	0	0	0
*M. cookei**	-	-	-	-	0	0	C	0	-	C	0	0	0
M. gymnotus	-	-	-	-	0	0	C	0	-	-	0	0	0
M. laticaudata	-	-	-	-	0	0	C	0	-	0	0	0	0
M. schultzei	-	-	-	-	0	0	C	0	-	-	0	-0-	
M. gymnopterus	-	-	-	-	0	0	C	0	-	-	0	-0-	

Table 5. Lateral Line and Cephalic Pore Conditions in Ophichthine Genera and Subgenera

Cephalic pore locations are illustrated in Figure 24. Abbreviations are: *, condition of type species unknown; +, present; -, absent; C, lateral line ossicles continuous; M, lateral line ossicles moderately separated at pores; S, lateral line ossicles separated at pores.

	tp2	pop3	pop4	Lateral Line Ossicles
Ophichthus	-	+	-	S
Echelus	-	+	-	S
Ophisurus	-	+	-	S
Pisodonophis	-	+	-	S
Quassiremus	-	+	-	S
*Cirrhimuraena**	-	+	-	S
Calamuraena	?	+	-	?
Jenkinsiella	-	-	-	S
Echiophis	-	+	-	S
Mystriophis	-	+	-	S
Aplatophis	-	-	-	S
*Brachysomophis**	-	-	-	S
Xyrias	-	-	-	?
Scytalichthys	-	-	-	S
Pogonophis	-	-	-	M
Evips	-	-	-	M
Leiuranus	-	-	-	M
Elapsopis	-	-	-	M
Phyllophichthus	-	-	-	S
Malvoliophis	-	-	-	M
Myrichthys	-	-	-	M
Apterichtus	+,-	+	+,-	C
Ichthyapus	+	+	+,-	C
Cirricaecula	+	+	+	C
Stictorhinus	+	+	-	C
Caecula	+	+	-	C
Yirrkala	+,-	-	-	C
Lamnostoma	-	-	-	C
Aprognathodon	-	-	-	C
Callechelys	-	-	-	C
Letharchus	-	-	-	C
Leuropharus	-	-	-	C
Paraletharchus	-	-	-	C
*Bascanichthys**	-	-	-	M
Allips	-	-	-	M
Phaenomonas	-	-	-	M
Ethadophis	-	-	-	M
Caralophia	-	-	-	S
Leptenchelys	-	-	-	?
Dalophis	-	-	-	M

Table 6. Vertebral Counts of Various Ophichthid Species

Data were obtained during the present study except as cited. The listing is arranged alphabetically by genus and species within each tribe. Counts include the hypural. "N" indicates number of nd v dua s

	Holotype	Range	Mean	N	Source
Benthenchelys cartieri		156-174	168.3	34	Castle, 1972
Ahlia egmontis			152	1	
Muraenichthys aoki	137				
Muraenichthys australis			152		Castle, 1965
Muraenichthys breviceps			164		Castle, 1965
Muraenichthys chilensis	149	148-153	150.9	12	McCosker, 1970
Muraenichthys cookei			130		Gosline, 1951a
Muraenichthys gymnotus		129-130	129.5	2	
Muraenichthys hattae	154				
Muraenichthys iredalei		126-127	126.5	2	
Muraenichthys macropterus		127-130	128.2	4	
Muraenichthys schultzei			122	2	
Muraenichthys thompsoni	128?	128-133	130.5	2	
Myrophis plumbeus		142-154			Blache, et al., 1970
Myrophis punctatus		138-145			Eldred, 1966
Myrophis vafer		146-150	147.8	5	
(holotype of *Hesperomyrus fryi*)	154?				
Neenchelys buitendijki		145-148			Mohamed, 1958
Pseudomyrophis micropinna	174				
Pseudomyrophis nimius		212-216	214	2	
Schismorhynchus labialis	136	134-138	136	6	
Schultzidia johnstonensis		145-149	151.2	5	
Schultzidia retropinnis (holotype of *Muraenichthys malaita*)	133				
Aprognathodon platyventris		150-155	152.5	2	
Callechelys bilinearis		161-163	162	2	
Callechelys cliffi	155	149-158	154.9	14	
Callechelys eristigmus	159	154-163	157.9	30	
Callechelys galapagensis	172	170-174	172	4	
Callechelys holochromus	166				
Callechelys leucopterus		162-165	164	4	Blache and Cadenat, 1971
Callechelys marmoratus		176-183	179	4	
(holotype of *Callechelys guichenoti*)	183				
Callechelys melanotaenius		200-205	203	5	
Callechelys muraena	141	141-144	142.5	2	
Callechelys nebulosus		158-159	158.7	3	
Callechelys perryae	178				Blache and Cadenat, 1971
Callechelys springeri	170	166-170	168	2	
Callechelys striatus			192	1	
Letharchus velifer	139	135-143	139.5	14	McCosker, 1974
Letharchus rosenblatti	151	144-151	148.4	20	McCosker, 1974
Leuropharus lasiops	135				
Paraletharchus opercularis	180	171-180	174.7	9	
Paraletharchus pacificus	166	156-167	160.4	15	
Apterichtus ansp		123-132		-	Böhlke, 1968
Apterichtus caecus			151	1	
Apterichtus equatorialis?[1] (holotype has 53 preanal vertebrae)			146	1	
Apterichtus flavicaudus		145-157	149.6	5	
Apterichtus gymnocelus			136	1	
Apterichtus kendalli		137-144			Böhlke, 1968
Apterichtus klazingai	140				
Caecula pterygera	126	126-130	128.6	8	Böhlke and McCosker, 1975
Cirricaecula johnsoni			119	1	
Ichthyapus acutirostris	133				Blache and Bauchot, 1972
Ichthyapus ophioneus	133	132-137	133.7	3	
Ichthyapus selachops		137-144	139.3	15	

1. The holotype of *Caecula equatorialis* Myers and Wade lacks a tail. The specimen recorded here, ANSP 117436, is from 3°15'S, 80°19'W, and was not compared with the type.

Table 6. Continued

	Holotype	Range	Mean	N	Source
Ichthyapus vulturis[2]	123				
from Palau, Tahiti, and Seychelles		117-127	121.8	12	
from Hawaii and Kure		120-124	122.2	4	
from Easter Island		130-134	132.3	9	
Lamnostoma kampeni			143	1	
Lamnostoma mindora	144				
Lamnostoma orientalis		134-137	135.3	3	
Lamnostoma philippinensis	153?				
Stictorhinus potamius	140	135-142	139.4	11	Böhlke and McCosker,
Yirrkala lumbricoides		151-154	152.5	2	
(paratype of *Yirrkala chaselingi*)			153		
Yirrkala tenuis			153	1	
Allips concolor	174				
Bascanichthys cecilae	226	225-226	225.5	2	Blache and Cadenat, 1
Bascanichthys congoensis	189	189-190	189.5	2	Blache and Cadenat, 1
Bascanichthys longissimus			212	-	Blache and Cadenat, 1
Bascanichthys myersi	215				
Bascanichthys panamensis			181	1	
Bascanichthys paulensis	191				
Bascanichthys tenuis	203				
Bascanichthys teres		181-184		-	Blache and Cadenat, 1
Caralophia loxochila		139-145	142.3	3	
Dalophis imberbis	152	148-159	152.2	14	Blache and Bauchot, 1
Ethadophis byrnei	189				
Ethadophis merenda	159				
Leptenchelys vermiformis	163				
Phaenomonas cooperae	270	243-270	256	8	
Phaenomonas pinnata	187	175-194	186.5	14	
Aplatophis chauliodus		110-111	110.5	2	
Brachysomophis henshawi			130	-	Gosline, 1951a
Brachysomophis sauropsis		119-125	121	4	
Cirrhimuraena macgregori			181	-	Gosline, 1951a
Cirrhimuraena taeniopterus			183	1	
Echelus myrus					
from the Mediterranean		151-155		-	Grassi, 1913
from the eastern tropical Atlantic		149-152		-	Blache, et al., 1970
Echelus pachyrhynchus	157	149-157		-	Blache, 1968
Echiophis intertinctus	132	132-143		-	Blache, 1971
Echiophis mordax			130		
Echiophis sp.[3]		132-139	135.6	14	
Elapsopis cyclorhinus		153-160	156.5	2	
Evips percinctus	132				
Leiuranus semicinctus		162-169	166.3	3	
(holotype of *Machaerenchelys phoenixensis*)	170				
Myrichthys bleekeri			196	1	
Myrichthys colubrinus		197-201	199	2	
Myrichthys maculosus					
from Hawaii and Midway		174-182	178.5	16	
from western Pacific		190-199	193.2	10	
Myrichthys oculatus		170-171	170.5	2	
Myrichthys pardalis	158	151-159		-	Blache and Cadenat, 1
Myrichthys xystrurus		149-163	152.5	20	
Mystriophis blastorhinos	142				Blache, 1971
Mystriophis crosnieri		136-144	140.7	57	Blache, 1971
Mystriophis rostellatus		154-158	155.5	13	Blache, 1971
Ophichthus altipinnis			173	1	
Ophichthus callaensis			153	1	
Ophichthus cruentifer			146	1	
Ophichthus erabo	155		155	2	
Ophichthus frontalis		144-157	149.4	7	
Ophichthus gomesi			141	-	Jordan and Davis, 189

2. Population differences in *Ichthyapus vulturis* are treated in Randall and McCosker (19
3. An undescribed species ranging from the Gulf of California to Panama.

Table 6. Continued

	Holotype	Range	Mean	N	Source
Ophichthus macrochir			144	-	Castle, 1965
Ophichthus ocellatus			134	-	Jordan and Davis, 1892
Ophichthus ophis					
from Brazil			162	1	
from eastern tropical Atlantic		161-170		-	Blache, in litt.
Ophichthus rhytidodermatoides			191	1	
Ophichthus triserialis		145-160	152.5	2	
Ophichthus uniserialis	152?				
Ophichthus urolophus			136	1	
Ophichthus zophochir		150-152	150.7	3	
Ophisurus serpens		200-208			Blache, in litt.
Phyllophichthus xenodontus		169-170	169.5	6	
Pisodonophis boro		171-173	172	2	
Pisodonophis cancrivorus			155	1	
Pisodonophis daspilotus	137?	137-138	137.5	2	
Pogonophis fossatus		166-171	168.5	2	
Quassiremus evionthas			153	1	
Quassiremus nothochir		139-142	140.8	4	
Scytalichthys miurus		143-149	146	4	
Xyrias revulsus	158				

Table 7. Characteristics of the Ophichthidae and Related Eel Families

Abbreviations are: F, fused; O, ossified; R, reduced; S, sutured; +, present; -, absent. Data are from this study and various sources, including McAllister (1968), Robins and Robins (1970, 1971), and Smith and Castle (1972).

	Frontal Condition	Frontal Commissure	Temporal Pore Canal	Gill Arch Ossification	Branchiostegal Rays (pairs)
Ophichthidae	F	+	+		
Ophichthinae				O	15-34
Myrophinae				R	20-49
Congridae	F	-	+	O	8-17
Muraenesocidae	F	-	+?	O	8-22
Macrocephenchelyidae	F	-	+	O	8
Dysommidae	F	-	-	R	9-16
Xenocongridae	S	-	+	R	12-21
Heterenchelyidae	S	-	+	O	11-14
Muraenidae	S	-	-	R	<10
Anguillidae	S	-	+	O	8-14

Table 8. Morphological and Meristic Characters of the Species of Callechelyini

Adapted from and expanded upon McCosker and Rosenblatt (1972, Table 5). Abbreviations are as follows: Δ, rounded mean value; *, from the holotype; +, present; -, absent; ?, condition not known. Postanal lengths in thousandths of total length.

	Postanal[Δ] Length	Vertebrae	Scapula	Urohyal	Branchiostegal Rays	Epihyal Ray Broadening
Aprognathodon platyventris	351	155[Δ]	+	simple	28	extreme
Leuropharus lasiops	405	135*	+	?	32?	no?
Letharchus velifer	400	149*	+	?	32	extreme
L. rosenblatti	428	151*	+	simple	34	extreme
Paraletharchus pacificus	352	166*	+	simple	32	yes
P. opercularis	392	180*	+	simple	30	yes
Callechelys nebulosus	408	159[Δ]	+	simple	29	yes
C. springeri	350	170*	+	simple	25?	yes
C. bilinearis	364	162[Δ]	+	forked	27	no
C. cliffi	434	155*	+	forked	26	no
C. galapagensis	444	172*	+	forked	27	no
C. luteus	415	213	+	forked	27	no
C. muraena	385	141*	+	forked	23?	no
C. marmoratus	345	180[Δ]	-	simple	29	no
C. eristigmus	295	158*	-	simple	31	no
C. melanotaenius	282	203[Δ]	-	simple	29	no
C. striatus	304	192	-	simple	26	no
C. perryae	319	178*	-	simple	24	no
C. leucopterus	453	164[Δ]	?	?	?	?
C. holochromus	333	166*	-	simple	?	yes
C. bitaeniatus	385	?	?	?	?	?

Table 9. Characteristics of the Species of Callechelyini Used in Programs REGROUP and WVGM

I. Meristics

Vertebrae: 130-139; 140-149; 150-159; 160-169; 170-179; 180-189; 190-199; 200-209; 210-219
Branchiostegal rays: 22-23; 24-25; 26-27; 28-29; 30-31; 32-33; 34-35
Supraorbital pores: 3 or 4

II. External Morphology

Postanal length: 275-299; 300-324; 325-349; 350-374; 375-399; 400-424; 425-449; 450-474
Anal fin: present or absent
Gill opening "pocket": present or absent
Underside of snout: grooved, slightly grooved or ungrooved
Snout: blunt or conical; papillate or smooth
Anterior nostril: tubular or not tubular

III. Internal Morphology

DFO: above supraoccipital or above epiotics
Neurocranium: rounded or depressed
Intermaxillary teeth: present or absent
Urohyal: forked, simple and cartilaginous or simple and ossified
Hyoid: inflexible along CH-EH suture, slightly flexible or well separated
Hypohyals: present or absent
Vomerine teeth: present or absent
Scapula (?): present or absent
Epihyal rays: broadened basally, moderately broadened or slender
Third hypobranchial: ossified or cartilaginous

IV. Coloration

Mottled or weakly spotted
Strongly spotted
Longitudinally banded
Uniform body (fins may contrast)

Table 10. Distribution of Certain Ophichthid Genera

Refer to text for discussion of those genera marked with an asterisk.

	I. Circumtropical	
Apterichtus	*Bascanichthys*	*Callechelys*
Ichthyapus	*Myrichthys*	*Myrophis*
	Ophichthus	
	II. Restricted to Indo-Pacific	
Achirophichthys	*Allips*	*Benthenchelys*
Brachysomophis	*Caecula*	*Cirrhimuraena*
Cirricaecula	*Elapsopis*	*Evips*
Lamnostoma	*Leiuranus*	*Malvoliophis*
*Muraenichthys**	*Neenchelys*	*Schismorhynchus*
Schultzidia	*Xyrias*	*Yirrkala*
	III. Restricted to New World	
*Echiophis**	*Letharchus*	*Pseudomyrophis*
	Quassiremus	
	IV. Restricted to Eastern Pacific	
Ethadophis	*Leptenchelys*	*Leuropharus*
Paraletharchus	*Pogonophis*	*Scytalichthys*
	V. Restricted to Western Atlantic	
Ahlia	*Aprognathodon*	*Caralophia*
Gordiichthys	*Stictorhinus*	
	VI. Restricted to Eastern Atlantic and Mediterranean	
Dalophis	*Echelus*	*Mystriophis*

INDEX TO GENERA AND SPECIES
(Included are recognized species and valid and invalid genera)